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Experimental Investigations Into Effects Of Climate Change On High Arctic Plants

by

Michael Hunt Jones

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Renewable Resources

Edmonton, Alberta

Spring 1995

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Michael Hunt Jones

31 JANUARY 1995

INSTITUTE OF ARCTIC & ALPINE RESEARCH
UNIVERSITY OF COLORADO
BOULDER, COLORADO, USA

There is something fascinating about science. One gets such a wholesale return of conjecture out of a trifling investment of fact.

-- Mark Twain
1874

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Experimental Investigations Into Effects Of Climate Change On High Arctic Plants** submitted by Michael Hunt Jones in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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January 31, 1995

Abstract

The purpose of this research was to describe the initial, short-term responses of high arctic plant species to experimental conditions simulating predicted climate changes. This work was conducted at Alexandra Fiord on Ellesmere Island, Canada, as part of the International Tundra Experiment (ITEX).

Beginning in 1992, tundra soil was warmed up to 6°C above control plots using small, open-top greenhouses. For the arctic willow, Salix arctica, catkin and leaf fascicle lengths, stem increments, and specific leaf areas were greater for experimentally warmed plants, and the effect was substantially more pronounced for willows in a dry (vs. wet) community over three seasons. Reproduction and phenology were only slightly affected by warming. There was evidence of a cumulative effect of warming over time on most of the variables examined. Diurnal gas exchange, examined in 1992 and 1993, was highly dependent upon the sex of the plant and the habitat in which it grew. In the dry habitat, warming enhanced net assimilation (NA) in females but depressed it in males; stomatal conductance (g_s) was unaffected by warming. In the wet habitat, NA in female willows was depressed by warming but and enhanced in males; g_s was depressed in both sexes. In controlled environments, elevated atmospheric CO_2 and temperature had a significant, positive effect on NA, g_s, dark respiration, and water use efficiency in S. arctica grown under well-watered conditions. No downward regulation of NA was observed over time, and leaf age had little effect on photosynthesis. With soil drying, NA increased at

high CO_2 concentrations, but remained unchanged at ambient concentrations. Constant C_i/C_a ratios indicated stomatal sensitivity to increased carbon demand.

Diurnal gas exchange was examined in three sedge species on hummocks and in hollows in the wet community during 1992 and 1993. Experimental warming significantly depressed NA in the sedge Eriophorum angustifolium triste, but differences between hummock and hollow microsites were minimal. In contrast, experimental warming had little effect on Carex aquatilis stans, but plants growing on hummocks had significantly higher NA than plants in the hollows.

Preface

Throughout this dissertation the term "we" (first person plural) appears instead of the more usual "I" (first person singular), and occurs with the permission of my supervising committee. It is archaic, I believe, to write this dissertation using "I" throughout, and then subsequently publish manuscripts using "we", when the co-authors behind the work are really the same in both cases. By referring to the collective "we" in the body of this work, I wish to make it clear to readers that (i) this work is, in fact, an explicitly collaborative work with my supervisors SEM and GHRH, and also with my other committee member JH; and (ii) all publications resulting from this work will include SEM and GHRH as co-authors.

Acknowledgments

The task of completing a graduate degree is a large one, and I believe that the pleasures along the way-and those to come-from associations with particularly thoughtful and creative individuals far surpass the drawbacks and often substantial sacrifices of the effort. Yet with as much as I have invested in this dissertation, my efforts reflect but a portion of that given by many others to make this work successful, and it is with gratitude that I honour their contributions.

Foremost is Dr. Ellen Macdonald, who provided the constancy of her critical guidance, as well as her moral and logistical support, with true munificence and gentleness of spirit. Dr. Greg Henry generously incorporated me into his high arctic research, and shared with me the breadth of his knowledge and love for those wondrous landscapes. Together these two intelligent, energetic, and insightful people provide the best sort of models I know for critical thinking and evaluation, thoughtful planning, excellence in writing, and joy in living. We have shared some truly good times together in the far north and in these temperate latitudes. Without the teamwork of these co-supervisors, neither the research nor the graduate degree would have been possible. It is to them I owe the greatest thanks, particularly for their kind patience, and give it with the greatest of respect.

The other member of my supervisory committee is Dr. John Hoddinott, and I thank him for fruitful discussions and logistical assistance, as well as for help in recognizing and slaying some of the demons that come with learning self-confidence.

Another individual to whom I owe a unique thanks is Dr. Josef Svoboda, who laid the foundations for much of the contemporary high arctic vegetation research, and who has become not only a friend but a model for a certain kind of courage and conviction. Additionally, I wish to thank Dr. Mark Dale for his advice and sense of humour.

Another group of individuals deserves just as much thanks and acknowledgment, for without their willingness to share their knowledge and support, this thesis, like most others, I suspect, probably would not occur. Those people are my office-mates of these three years and more, who, as graduate students in their own right, taught me most of the things I needed to know, and shared their homes, food, and most of all their friendship. To Ken Greenway, Uldis Silins, Simon Landhäusser, Barb Thomas, and Kevin Astridge, my heartfelt thanks.

A very large list of people must also be recognized for varied and multitudinous contributions to this research, and sometimes to the sanity of this researcher. The good Arctic companionship and intellectual talents of fellow graduate students Jill Johnstone, Glenda Jones, Adrian deBruyn, Dean Morewood, Doris Nabert, and Colin Young, are much appreciated, and it is with additional pleasure that I thank Esther Levesque for sharing her wonderful *joie de vivre*. Much hard work in the field or lab, and some excellent entertainment as well, was provided by Rosalind Barrington-Leigh, Shawn Francis, Petra Lange, Lee Martens, Marge Meijer, Brett Purdy, Thor Smestad, Kristy Trainor, Pat Williston, and Sonja Winkleman; I also thank the University of Alberta phytotron, greenhouse, and farm crews. A special thanks goes to Sandy Akavak of Lake Harbor, who taught us something more about the Arctic. Information and material provided by Dr. Todd Dawson, Dr. Sylvia Edlund, Dr. Warren Gold, and other researchers and field crews at Sverdrup Pass and Hotweather Creek are greatly appreciated.

Most of all, however, I wish to express my gratitude to Jody Carter, my wife and friend, for her exceptional love and support throughout these years, and even more for taking on the additional responsibilities of being the only parent while I was relishing the pleasures of the High Arctic. Jody always reassured me that she took pleasure from knowing I was working in a place I love, however far away. But I also know that her heart yearned to be in the North too. It is my hope that Jody and I can share with our children, Courtney Wren Carter Jones and Gavin Alexander Carter Jones, the kinds of joys and

freedoms and wonder at life that we have known together in our sauntering through wild places.

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CHAPTER 1

General Introduction

Global change

If the earth's climate changes as predicted over the coming century, the effects on natural ecosystems are likely to be pronounced. It is not so much the certainty of future change which currently arouses our interest and concern. Indeed, historical analogs from ice core data, dendrochronology, and palynology indicate that the earth's climate has changed dramatically over long time spans (Schneider 1993), and the paleoecological record indicates that plant and animal species have responded by adapting, migrating, or by becoming extinct (Geber and Dawson 1993, Hoffmann and Blows 1993, Holsinger 1993). Even the relatively short-term temperature decline of the Little Ice Age had significant, long-lasting effects on arctic plant communities (Bergsma et al. 1984). Rather, it is the rate at which changes are occurring - and their association with anthropogenic disturbances - which raise important questions regarding the magnitude of the impacts of global change. Thus, global change encompasses not just apparent and predicted climatic changes, but landscape changes as well, including habitat loss, ecological invasions, and other anthropogenic disturbances including pollution. There is a perceived potential for large-scale changes in community structure and dynamics, and for environmental catastrophe facilitated by the interdependence of species within ecosystems (Kareiva et al. 1993).

It was the correlation between rise in global temperature and increases in anthropogenic greenhouse gases since the beginning of the Industrial Revolution which has stimulated the current concern regarding global change. Over the last 130 years, the global atmospheric CO_2 concentration has risen from about 275 $\mu mol\ mol^{-1}$ to more than 355 $\mu mol\ mol^{-1}$ today (Neftel et al. 1994). At Mauna Loa, Hawaii, where the longest continuous CO_2 measurements have been recorded in a pristine environment, the atmospheric CO_2 concentration has risen from 316 $\mu mol\ mol^{-1}$ since 1959 (Keeling and

Whorf 1994). Since the 1920's, mean global air temperature at the earth's surface has risen about 0.5°C (Schneider 1993), and predictions based on several general circulation models (GCMs) of climate change suggest that the average "best case" scenario for global warming will be approximately 2.5°C before the end of the next century (Schneider 1993). Although the relationship between greenhouse gases and temperature is unequivocal, attributing increased global temperature to elevated greenhouse gases is less certain because of natural climatic variability. The evidence has nevertheless compelled scientists and policymakers alike to consider seriously the potential effects of rapid climatic changes.

Climate change and Arctic ecosystems

At high latitudes, particularly in the Arctic, increases in temperature could be more pronounced than those in any other region of the globe. Based on GCM predictions, winter temperatures in the Canadian Arctic Archipelago could increase by 6-14°C, while summer temperatures could rise 1-5°C (Maxwell 1992). It is important to bear in mind that any changes in temperature will be driven by elevated atmospheric CO_2 concentrations, and that direct effects of CO_2 and temperature are likely to be modified substantially by other, indirect effects of climate change on arctic environments.

For example, warmer spring temperatures could result in a longer growing season, although increased precipitation caused by warmer air could increase snowfall and therefore delay snowmelt and effectively shorten the growing season. Elevated soil temperatures would increase the depth of the active layer, altering soil moisture and nutrient availability through increased mineralization and effects on soil heterotrophs and mycorrhizae. Competitive interactions among individuals and species, including plant-herbivore interactions, and changes in successional patterns, all have the potential to significantly alter tundra structure and function (Chapin et al. 1992a). Evolutionary potential may be influenced not only by the longevity of arctic vegetation and the current restrictions on sexual reproduction, but also by

apparently strong ecotypic differentiation in the arctic (McGraw and Fetcher 1992). Moreover, alterations in plant communities will undoubtedly have strong positive and negative feedback roles on ecosystem function. For example, increased aboveground biomass and litter could eventually negate increases in thaw depth through shading and insulation (Chapin et al. 1992a). Although the magnitude of most of the primary and secondary effects of elevated CO_2 and temperature are uncertain, it is nevertheless clear that the potential for changes in arctic ecosystems is large.

One of the major concerns regarding Arctic ecosystem responses to climate change involves CO_2 flux. Arctic and boreal ecosystems contain approximately 25% of the total world terrestrial carbon pool and, because of cold, often anaerobic soil conditions, have been strong sinks for organic carbon (Oechel and Vourlitis 1994). Within the last decade, however, tussock and wet sedge tundra in Alaska have been found to become sources, rather than sinks, of atmospheric CO_2 (Oechel and Vourlitis 1994). Increased temperature and active layer depth, coupled with decreased soil moisture, have enhanced decomposition rates, and raise concerns about positive feedback between arctic carbon stores and increasing atmospheric CO_2 concentrations. Carbon flux provides an indication of whole-ecosystem response to climatic changes since it integrates productivity and respiration with the processes that regulate ecosystem function (Oechel and Vourlitis 1994).

Although the Arctic has received considerable attention from plant ecologists, including the intensive descriptive work of the International Biological Program (Bliss et al. 1981), only relatively recently has experimental research examined the impacts of environmental manipulations on tundra species and communities. With increasing concern regarding the impacts of global climate change, interest in arctic ecosystems has grown. One reason for this is that arctic plants exist at the limit of their current ranges in these extreme environments. If climatic changes are more pronounced in the arctic than in other biomes, responses to these changes should be readily apparent. In addition, biodiversity is low in tundra systems, and the structural and

spatial scales at which tundra species are found facilitate study of both plant physiology and ecosystem responses simultaneously (Chapin et al. 1992).

Only a few studies have examined the direct responses of elevated CO_2 coupled with increased temperature on arctic species (Tissue and Oechel 1987) or ecosystems (Hilbert et al. 1987, Grulke et al. 1990, Oechel et al. 1992). These studies have shown that photosynthesis is initially stimulated by elevated CO_2 and temperature, but that downward regulation returned carbon fixation to pre-treatment levels after periods of time ranging from a few weeks to three years. The cause of this decline is unclear. Photosynthesis and growth of other arctic species in response to enhanced CO_2 in controlled environments have been found to be dependent upon soil nutrient levels, suggesting that climatic changes unaccompanied by improved soil nutrient levels would have little impact on tundra production or composition (Oberbauer et al. 1986).

Other studies which manipulated temperature, nutrients, light or water availability for arctic species (Chapin 1983, Chapin 1991, Chapin and Shaver 1985, Henry et al. 1986, Wookey et al. 1993, Parsons et al. 1994, Woodley and Svoboda 1994) demonstrated that responses vary substantially by species, habitats, and the type, magnitude, and duration of the environmental manipulations. In Alaskan tundra, community productivity is relatively stable from year to year, even though species have markedly different responses to seasonal climate variability (Chapin and Shaver 1985). Tundra production in arctic Scandinavia (Parsons et al. 1994) and alpine, continental North America (Walker et al. 1994) is more sensitive to climatic variability. The response dynamics of species, communities, and ecosystems to the kinds of environmental changes predicted are therefore not at all certain.

International Tundra Experiment

The International Tundra Experiment (ITEX) was formed in recognition of the vulnerability of arctic ecosystems to predicted climatic changes, and of the importance of examining these changes across the entire circumpolar north. In late 1990, a group of more than 50 scientists, representing all arctic rim nations as well as those with active arctic interests and research programs,

convened a workshop at the Kellogg Biological Station, Michigan State University, and agreed to develop and implement a common experiment focusing on species-level responses to environmental manipulations simulating climate change. Further meetings were held, and a formal experimental design and protocol were established at a meeting held in Boulder, CO in 1992.

ITEX participants use common experimental design, measurement, and data recording protocols, making comparisons of results possible across all research sites. Three general levels of investigations are being conducted: (i) long-term monitoring of climate and the phenology, growth, and reproduction of selected tundra plant species; (ii) use of simple field experiments to alter growing season temperature and growing season length; and (iii) more sophisticated field and controlled environment experiments (Molau 1993). The basic experimental field manipulation involves the use of small, transparent fiberglass, open-top chambers (OTCs) which block the wind and allow the air within to warm (Marion et al. 1993; Greg Henry and the author were the designers of the OTC accepted as the ITEX standard). Carbon dioxide concentrations are not manipulated in the OTCs primarily because of the costs involved and the desire to make participation as broad as possible. To be formally recognized as an ITEX site, a minimum set of environmental and biotic variables must be monitored, at least the standard simple field experiment must be in place, and a commitment made for a minimum period of five years (Molau 1993).

Central support for the ITEX Secretariat and database are provided by the Danish Polar Center in Copenhagen, with additional financial support provided by the US Man and the Biosphere Program High Latitude Ecosystems Directorate and the Swedish Royal Academy of Sciences. Financial support for individual sites is secured by the principal investigators involved. ITEX research sites or programs are now in place in Canada, Denmark (including Greenland), Finland, Great Britain, Iceland, Norway, Russia, Sweden, Switzerland, and the US. Preliminary results from the first-established ITEX sites, including those in Canada, were presented at a meeting in St. Petersburg,

Russia, in 1994; more complete results will be published as a result of the next international ITEX meeting in Ottawa in April 1995. If a planned funding proposal to the US National Science Foundation is successful, integration and synthesis of all short-term ITEX data will be initiated in 1995. Only in the arctic can experimental replication be conducted across such a large geographic area, not only within a single biome but also on the same species within that biome; approximately 60% of Arctic species are common throughout circumarctic regions (Murray 1992, Walker 1994).

The present research

In this study, we examined the initial, short term responses of three high arctic tundra species to experimental manipulations which simulated global climate changes. The principal goal was to quantify the direct influence of enhanced temperature and atmospheric CO_2 on the arctic dwarf willow, Salix arctica, during the first three years of a long-term field experiment. We explicitly examined response variability introduced by sex and habitat, as well as different temporal scales, in order to broaden the ecological interpretation of the results. The study included three major components: (i) general autecology and (ii) diurnal gas exchange under experimentally warmed conditions in the field, and (iii) gas exchange under elevated CO_2 and temperature in controlled environments. In addition, we examined diurnal photosynthesis responses of three important sedge species, Carex aquatilis stans, Eriophorum angustifolium triste, and Carex membranacea, in hummock and hollow microsites and under experimentally warmed conditions.

This research was conducted as part of the International Tundra Experiment at Alexandra Fiord on Ellesmere Island in the Canadian High Arctic. Beginning in 1992, extensive arrays of OTCs and microclimate recording stations were established in six plant communities at Alexandra Fiord. Related experimental manipulations and observational studies involving a number of tundra species were also established. Together, these studies initiated a coordinated, long-term investigation into species- and ecosystem-level responses to global climate change, and involve a number of investigators and

graduate students. Previous investigations of the ecology and climate of the Alexandra Fiord lowland, some of which is still ongoing (Svoboda and Freedman 1994), provide valuable supporting information for the current research.

The principle focus of the work described here was the dwarf arctic willow, Salix arctica Pall. This deciduous, dioecious species is widespread throughout the circumpolar north, and is the only willow found north of 80° latitude (Porsild and Cody 1980). Salix arctica is an important component of many high arctic plant communities, and provides forage for vertebrate grazers, including muskox, arctic hare, Peary caribou, and collared lemming, as well as for several invertebrate species. We examined willows in two plant communities on the lowland at Alexandra Fiord. One habitat is relatively xeric, and Salix arctica is the dominant vascular species in this community. The other habitat is a wet to mesic sedge meadow; in this habitat, willows are an important component but are restricted to hummocks. In addition, we examined the responses of both male and female willows. Previous research by Dawson and Bliss (1989a,b) demonstrated substantial differences in water relations between sexes and between wet and dry arctic habitats. We wanted to test whether sexual differences were apparent under experimentally warmed conditions in either of the two habitats described above.

Little previous research had been conducted on this species in North America, most of it descriptive (Sorensen 1941, Warren Wilson 1957, 1964, Savile 1979, Kevan 1990). Experimental or more detailed work included that by Woodley and Svoboda (1994), who examined S. arctica phenology and foliar nutrients in response to experimental warming, fertilization, and the timing of snowmelt at Alexandra Fiord, finding that this species responded substantially to these treatments. Dawson and Bliss (1989a,b) examined water relations among arctic and alpine populations of S. arctica. Kukal and Dawson (1989) examined foliar nutrients, nonstructural carbohydrate content, and secondary compounds in Salix arctica as part of a study of arctic woolly-bear caterpillars (Gynaephora groenlandica). Finally, research by Doris Nabert at Sverdrup Pass

on Ellesmere Island examined responses of this willow to grazing experiments (unpublished MSc research, Biology Department, Erindale College, University of Toronto).

In addition to Salix arctica, we examined three sedge species in the meadow, including Eriophorum angustifolium triste Honck., Carex aquatilis stans (Drej.) Boott, and Carex membranacea Hook. These species dominate the sedge meadows in the High Arctic, and are important food sources for tundra grazers including snow geese and muskox. The microtopography of the sedge meadows at Alexandra Fiord is composed of hummocks and hollows and, in contrast to the willows growing in the meadow, sedges grow in both microsites. We postulated that characteristic differences in microsite environments would have an impact on sedge performance because hummocks are raised above the saturated soils of the hollows and provide substantially warmer growing conditions.

Growth, phenology, and reproductive characteristics of male and female willows were measured over the course of the first three seasons of experimental treatment in order to identify and quantify broad autecological responses to warming (Chapter 2). Low summer temperature is one of the main environmental factors that constrain plant and soil processes in arctic habitats (Chapin and Shaver 1985, Billings 1987, Nadelhoffer et al. 1991). Based on other research (e.g., Wookey et al. 1993, Woodley and Svoboda 1994), we anticipated that S. arctica would probably respond to ameliorated growing temperature by altering the timing and, possibly, the magnitude of its growth and reproductive activities.

During the first season, we measured baseline diurnal gas exchange of control plants of both willow sexes growing in both the wet and dry habitats, and of the three sedge species in both microsites in the meadow. In the second year we included experimentally warmed willows (Chapter 3), as well as Carex aquatilis stans and Eriophorum angustifolium triste (Chapter 4). We were aware of only one other published field gas exchange study conducted in the High Arctic (Mayo et al. 1977), and wanted to determine whether diurnal gas

exchange patterns existed given the 24 hour sunlight regime during the height of the summer growing season. Furthermore, by examining photosynthesis and stomatal conductance in this manner, we were better able to determine how the willows were responding to experimental warming throughout their diurnal cycles.

The final component of this research involved growing Salix arctica in a factorial experiment in which atmospheric CO_2 and temperature regimes reflected current and potential future climatic conditions (Chapter 5). Examining plant responses under combinations of these factors is important, since substantial changes in arctic growing season temperatures will be driven by elevated atmospheric CO_2 and other radiatively active greenhouse gases (Maxwell 1992); measuring photosynthesis under elevated temperature alone gives an incomplete understanding of responses likely under global change (Long 1991). Based on the results of our field work and those of other studies, we expected that Salix arctica would probably respond favorably to elevated CO_2 and temperature, and that soil drying would have little effect, at least initially, on photosynthesis.

It is clear from the available evidence that not all arctic or alpine tundra species respond similarly to the kinds of environmental changes predicted to occur. Differences in life history characteristics, including longevity, but especially reproductive habit and potential, will be particularly important in determining how tundra species may adjust or adapt to future climates (McGraw and Fetcher 1992, Geber and Dawson 1993). The results of the studies reported here offer a significant contribution to our understanding of tundra vegetation, not only because extremely little experimental work had been conducted on high arctic vegetation in North America, but also because we explicitly examined response variability introduced by species and life form, sex, habitat, and microsite within habitat, as well as different temporal scales. If we are to build reasonable, mechanistic models of tundra ecosystem dynamics, then we need a detailed understanding of how many of their individual components function at multiple levels of organization (Chapin et

al.1992b, Pacala and Hurtt 1993). Together with current and future research at Alexandra Fiord, and elsewhere in the network of ITEX research sites, we should be able to understand much of the way tundra vegetation will respond to global change.

References

Bergsma, B. M., J. Svoboda, and B. Freedman. 1984. Entombed plant communities released by a retreating glacier at central Ellesmere Island, Canada. Arctic **31**:49-52.

Billings, W. D. 1987. Constraints to plant growth, reproduction, and establishment in arctic environments. Arctic and Alpine Research **19**:357-365.

Bliss, L. C., O. W. Heal, and J. J. Moore, editors. 1981. Tundra ecosystems. Cambridge University Press, Cambridge.

Chapin, F. S., III. 1983. Direct and indirect effects of temperature on arctic plants. Polar Biology **2**:47-52.

---. 1991. Integrated responses of plants to stress. BioScience **41**:29-36.

Chapin, F. S., III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver, and J. Svoboda. 1992a. Arctic plant physiological ecology in an ecosystem context. Pages 441-451 *in* F. S. III Chapin, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Chapin, F. S. III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver, and J. Svoboda. 1992b. Arctic plant physiological ecology: a challenge for the future. Pages 3-8 *in* F. S. Chapin, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology **66**:564-576.

Dawson, T. E., and L. C. Bliss. 1989a. Intraspecific variation in the water relations of Salix arctica, an arctic-alpine dwarf willow. Oecologia **79**:322-331.

---. 1989b. Patterns of water use and the tissue water relations in the dioecious shrub, Salix arctica: the physiological basis for habitat partitioning between the sexes. Oecologia **79**:332-343.

Geber, M. A., and T. E. Dawson. 1993. Evolutionary responses of plants to global change. Pages 179-197 *in* P. M. Kareiva, J. G. Kingsolver and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, MA, USA.

Grulke, N. E., G. H. Riechers, W. C. Oechel, U. Hjelm, and C. Jaeger. 1990. Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. Oecologia **83**:485-494.

Henry, G. H. R., B. Freedman, and J. Svoboda. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. Canadian Journal of Botany **64**:2502-2507.

Hilbert, D. W., T. I. Prudhomme, and W. C. Oechel. 1987. Response of tussock tundra to elevated carbon dioxide regimes: analysis of ecosystem CO_2 flux through nonlinear modeling. Oecologia **72**:466-472.

Hoffmann, A. A., and M. W. Blows. 1993. Evolutionary genetics and climatic change: will animals adapt to global warming? Pages 165-178 *in* P. M. Kareiva, J. G. Kingsolver and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, MA, USA.

Holsinger, K. S. 1993. The evolutionary dynamics of fragmented plant populations. Pages 198-216 *in* P. M. Kareiva, J. G. Kingsolver and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, MA, USA.

Kareiva, P. M., J. G. Kingsolver, and R. B. Huey, editors. 1993. Biotic interactions and global change. Sinauer, Sunderland, MA, USA.

Keeling, C. D., and T. P. Whorf. 1994. Atmospheric CO_2 records from sites in the SIO air sampling network. Pages 16-26 *in* T. A. Boden, D. P. Kaiser, R. J. Sepanski and F. W. Stoss, editors. Trends '93: A compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA.

Kevan, P. G. 1990. Sexual differences in temperatures of blossoms on a dioecious plant, Salix arctica: significance for life in the arctic. Arctic and Alpine Research **22**:283-289.

Kukal, O., and T. E. Dawson. 1989. Temperature and food quality influences feeding behavior, assimilation efficiency and growth rate of arctic woolly-bear caterpillars. Oecologia **79**:526-532.

Long, S. P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: has its importance been underestimated? Plant, Cell and Environment **14**:729-739.

Marion, G. M., G. H. R. Henry, P. Molgaard, W. C. Oechel, M. H. Jones, and G. L. Vourlitis. 1993. Open-top devices for manipulating field temperatures in tundra ecosystems. Lunardini,V.J. and S.L. Bowen, eds. Proceedings, Fourth International Symposium on Thermal Engineering and Science for Cold Regions, 28 Sept.-1 Oct. 1993. U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH. (205-210)

Maxwell, B. 1992. Arctic climate: potential for change under global warming. Pages 11-34 *in* F. S. III Chapin, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, CA.

Mayo, J. M., A. P. Hartgerink, D. G. Despain, R. G. Thompson, E. M. Z. Bakker, and S. D. Nelson. 1977. Gas exchange studies of Carex and Dryas, Truelove Lowland. Pages 265-280 *in* L. C. Bliss, editor. Truelove Lowland, Devon Island, Canada: a High Arctic ecosystem. University of Alberta Press, Edmonton.

McGraw, J. B., and N. Fetcher. 1992. Response of tundra plant populations to climatic change. Pages 359-376 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Molau, U., editor. 1993. The International Tundra Experiment Manual. Danish Polar Center, Copenhagen.

Murray, D. F. 1992. Vascular plant diversity in Alaskan arctic tundra. Northwest Environmental Journal **8**:29-52.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and J. A. Laundre. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology **72**:242-253.

Neftel, A., H. Friedli, E. Moor, H. Lõtscher, H. Oeschger, U. Siegenthaler, and B. Stauffer. 1994. Historical CO_2 record from the Siple Station ice core. Pages 11-14 *in* T. A. Boden, D. P. Kaiser, R. J. Sepanski and F. W. Stoss, editors. Trends '93: A compendium of data on global change, ORNL/CDIAC-65 Edition. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA.

Oberbauer, S. F., N. Sionit, S. J. Hastings, and W. C. Oechel. 1986. Effects of CO2 enrichment and nutrition on growth, photosynthesis, and nutrient concentration of Alaskan tundra plant species. Canadian Journal of Botany **64**:2993-2998.

Oechel, W. C., and G. L. Vourlitis. 1994. The effects of climate change on land-atmosphere feedbacks in arctic tundra regions. Trends in Ecology and Evolution **9**:324-329.

Oechel, W. C., G. Riechers, W. T. Lawrence, T. we. Prudhomme, N. Grulke, and S. J. Hastings. 1992. 'CO_2LT' an automated, null-balance system for studying the effects of elevated CO_2 and global climate change on unmanaged ecosystems. Functional Ecology **6**:86-100.

Pacala, S. W., and G. C. Hurtt. 1993. Terrestrial vegetation and climate change: integrating models and experiments. Pages 57-74 *in* P. M. Kareiva, J. G. Kingsolver and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, MA, USA.

Parsons, A. N., J. M. Welker, P. A. Wookey, M. C. Press, T. V. Callaghan, and J. A. Lee. 1994. Growth responses of four sub-arctic dwarf shrubs to simulated environmental change. Journal of Ecology **82**:307-318.

Porsild, A. E., and W. J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. National Museums of Canada, Ottawa.

Savile, D. B. O. 1979. Ring counts in Salix arctica from northern Ellesmere Island. Canadian Field-Naturalist **93**:81-82.

Schneider, S. H. 1993. Scenarios of global warming. Pages 9-23 *in* P. M. Kareiva, J. G. Kingsolver and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, MA, USA.

Sorensen, T. 1941. Temperature relations and penology of the northeast Greenland flowering plants. Meddelelser om Gronland **125**:1-307.

Svoboda, J., and B. Freedman, editors. 1994. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus University Publications, Toronto.

Tissue, D. T., and W. C. Oechel. 1987. Response of Eriophorum vaginatum to elevated CO_2 and temperature in the Alaskan tussock tundra. Ecology **68**:401-410.

Walker, M. D. 1994. Patterns of arctic plant community diversity. *in* F. S. III Chapin and C. Kõrner, editors. Arctic biodiversity and global change. Springer-Verlag, New York. in press.

Walker, M. D., P. J. Webber, E. H. Arnold, and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology **75**:393-408.

Warren Wilson, J. 1957. Observations on the temperatures of arctic plants and their environment. Journal of Ecology **45**:499-531.

---. 1964. Annual growth of Salix arctica in the high-arctic. Annals of Botany **28**:71-76.

Woodley, E. J., and J. Svoboda. 1994. Effects of habitat on variations of phenology an nutrient concentration among four common plant species of the Alexandra Fiord Lowland. Pages 157-176 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, Ontario.

Wookey, P. A., A. N. Parsons, J. M. Welker, J. A. Potter, T. V. Callaghan, J. A. Lee, and M. C. Press. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. Oikos **67**:490-502.

CHAPTER 2

Growth and reproduction of Salix arctica at Alexandra Fiord, Ellesmere Island: responses to experimental warming

Introduction

How arctic species will respond to climatic changes over the coming century is uncertain. Elevated atmospheric CO_2 and other radiatively active gases may lead to a 4°C increase in summer temperatures (Maxwell 1992) plus an array of other environmental changes including shifts in precipitation, growing season length, thaw depth, soil hydrology and nutrient dynamics (Chapin et al. 1992). Billings (1992) emphasizes that tundra species share one common, adaptive trait, i.e., the ability to grow, metabolize, and reproduce at low temperature. However, temperature has stronger indirect effects on arctic species by controlling the rates at which resources become available, than direct effects on physiological processes (Kielland and Chapin 1992). For example, low soil temperature constrains nutrient mineralization and availability in arctic soils (Nadelhoffer et al. 1991), but photosynthesis occurs at relatively high rates over a broad temperature range in most arctic species, and is less temperature sensitive than in temperate species (Semikhatova et al. 1992). Studies of arctic vegetation show that species respond individualistically to environmental manipulations (Chapin and Shaver 1985, Henry et al. 1986). In high arctic environments, some species exhibited increased growth (Henry 1987, Havstrõm et al. 1993) or flowering and reproduction (Henry 1987, Wookey et al. 1993) when summer temperatures were raised slightly in field experiments. In low or sub-arctic regions, however, enhanced growing season temperature often had little or no effect on growth (Parsons et al. 1994)

Experimental manipulations explicitly simulating climate change have not previously been conducted on high arctic plant species in North America, and few studies have examined the ecology of willows at high latitudes in general. The purpose of this study was to examine the short-term growth and reproductive responses of the arctic willow, Salix arctica, to experimental

warming in the range of temperatures anticipated over the coming century. Salix arctica is an important species in many high arctic plant communities, and provides forage for both vertebrate and invertebrate herbivores. We anticipated that S. arctica would probably respond to ameliorated growing temperature by altering the timing and, possibly, the magnitude of its growth and reproductive capabilities. However, we were uncertain whether male and female plants respond similarly to warming, and whether plants in either of two habitat representing markedly different growing conditions, would respond differently. We quantified growth responses during the first three growing seasons of a long-term field experiment on Ellesmere Island in the Canadian High Arctic; this research was conducted as part of the International Tundra Experiment (ITEX).

Methods

Species and study site

The prostrate, dioecious shrub Salix arctica is common in circumpolar regions and, in North America, is the only willow species present north of 80° latitude (Porsild and Cody 1980). We examined this species on the lowland at Alexandra Fiord, Ellesmere Island (78°53'N, 75°55'W) in the Canadian Arctic Archipelago. This lowland is a polar oasis, with generally warmer temperatures and more soil moisture than polar desert or semi-desert environments, which results in greater plant cover and productivity. An extensive description of the ecology of the Alexandra Fiord lowland can be found in Svoboda and Freedman (1994). We examined plants in two habitats. One (DRY) is relatively xeric, characterized by minimal snow deposition, early snowmelt, deep early-season active layer, and dry sandy and peaty soils (Muc et al. 1994). Salix arctica is the dominant species in this location. The second habitat (WET) is a wet sedge meadow with relatively later snowmelt, cold soils with a later-developing active layer, and typically with surface water flowing most of the growing season. Willows are an important component in this habitat but are restricted to hummocks (Henry et al. 1990).

Experimental warming chambers

Plants were subjected to passive warming beginning mid-June 1992 using open-top warming chambers (OTCs). OTCs are 1.5 m diameter hexagons, with 0.5m high sides inclined inwardly at 60° from horizontal, and are made of translucent fiberglass sheets used in greenhouse applications (Sun-Lite HP, Solar Components Corporation, Manchester, NH, USA). See Marion et al. (1993) for construction and additional OTC performance details. OTCs were placed over a randomly-selected subset of male and female plants in close enough proximity to enclose one plant of each sex within each OTC, but > 30 cm from chamber edges. Control plants were also randomly selected from male and female pairs within approximately 1m of each other in nearby plots. Ten OTCs and ten control plots were permanently established in each habitat for growth-related measures. An additional four OTCs in each habitat, each enclosing one male and one female willow, were established for a one-time examination of reproductive effort, measured in 1994.

In 1992, single mid-afternoon measurements of soil (3 cm) and air (10 cm) temperature were recorded daily in OTCs and control plots in both habitats using thermocouples and a microvoltmeter (N=12: 3 OTCs and 3 control plots in each habitat). In an adjacent community not part of this study, continuous, year-round micrometeorological measurements were recorded in six OTCs and six control plots using an array of three soil (3 cm) thermocouples/plot and a datalogging system (CR10, multiplexer, and storage module, Campbell Scientific, Logan, UT, USA). Ultrasonic snow depth sensors (Campbell Scientific Canada Corp., Edmonton, AB, Canada) positioned over three OTCs and three control plots continuously recorded snow depths. In 1993, an identical year-round data acquisition system was established in the dry habitat examined in this study, but also included one air (10 cm) termocouple/plot. During the summer of 1994, soil temperatures (3 cm) were continuously recorded in the wet meadow using an array of thermistors and datalogging systems (Pocketloggers, Pace Scientific, Charlotte, NC, USA). General climate data for Alexandra Fiord lowland can be found in Appendix A and in Labine (1994).

Plant measurements

Growth and phenology were measured for male and female plants in and out of OTCs in both habitats during 1992, 1993, and 1994. Catkin length was measured to the nearest mm from the axis of the stem and catkin peduncle, or, if a terminal catkin, from the terminal bud scar to the tip of the catkin. Leaf fascicles, rather than individual leaves, were measured from the terminal bud scar to the tip of the most distal leaf. Typically 7-9 individual leaves were produced from a single bud, and developed sequentially over several weeks. The earliest leaves were small and reached full expansion within a few days of bud break; subsequent leaves were much larger, sometimes by as much as an order of magnitude.

Initially, three catkins and three leaf fascicles were measured on each plant, and we attempted to measure leaves on the same branches in subsequent years. However, buds sometimes did not develop or were damaged by frost or invertebrate herbivores, and the number of catkins available or suitable for measurement varied among years, altering the consistency of our annual sample sizes. Final sample sizes are found in Table 2.1. Annual stem increments (mm) were measured for all tagged branches in each year. Increments for 1992 and 1993 growth were measured in late August 1993, and 1994 stems were measured in late August 1994. Specific leaf areas ($m^2\ g^{-1}$, SLA) were calculated for leaves harvested on 30 June 1993, after gas exchange measurements, and for leaves harvested on 3 July 1994 specifically for SLA. Because leaf areas vary considerably with position in fascicle, we standardized by measuring the third leaf in each fascicle.

Reproductive effort (RE) was measured in early July 1994. Experimentally-warmed plants had been growing undisturbed in OTCs since June 1992, and control plants were randomly selected from nearby undisturbed tundra. Three willows of each sex in each treatment and habitat were examined, with the exception of experimentally warmed males in the wet meadow, which produced no catkins in 1994 and could therefore not be

included in the analysis. Because of the difficulty of excavating roots from areas of shallow active layer, only aboveground biomass was harvested. Material was subsequently sorted and dried to constant weight. Reproductive effort was then calculated as the ratio of catkin biomass to leaf biomass or to total aboveground biomass, measured after pollen release.

Female reproductive success was determined for willows in both habitats and treatments in 1993 and 1994, with as many as one catkin/OTC or control plot, if available. The number of total and filling capsules/catkin, and the number of total and green (apparently viable) ovules/capsule were quantified (as per Molau 1993). Because so few female catkins were produced in OTCs in the wet habitat in 1994; none were harvested for these measurements in order to leave intact a reasonable number for season-long growth measurements. Ovule counts were conducted under a microscope by submerging capsules in backlit petrie dishes with water and a drop of detergent. In order to determine whether longer catkins have greater reproductive potential, a regression of the number of staminate or pistillate flowers on catkin length was constructed from 75 control catkins of each sex collected from three major plant communities on the lowland (dwarf shrub-cushion plant; sedge-cushion plant-dwarf shrub; and dwarf shrub-graminoid (Muc et al. 1994)).

Seed germination was tested in the field and laboratory. Field germination trials were conducted in six 1 m^2 plots in each of the habitats. Plots were thoroughly tilled to a depth of 10 cm, and as much as possible of the original above and below ground biomass was removed; the soil surface was then smoothed by hand. Three plots in each habitat were warmed using 1 m diameter OTCs and the others serving as controls. The small OTCs warm the soil to the same extent as the 1.5 m diameter OTCs used for the other experiments. In mid-August 1992, seeds collected from non-experimental areas in the dry habitat were sown in one section of each germination plot (250/plot). Similarly, seeds collected in 1993 were sown in another section of the same plots in August of that year (100/plot). Germination and survival were examined during subsequent growing seasons. In addition, six unsown 1 m^2

plots, three in each habitat, served as controls for seedling recruitment from windblown seed; OTCs were not used in these plots.

Laboratory germination trials were conducted using seeds collected from Alexandra Fiord and other locations on Ellesmere Island. Prior to germination trials, seeds were kept cool (5-10°C), or were refrigerated at 2°C or -2°C for 5 months. Covered petrie dishes lined with moistened filter paper were kept in growth cabinets at 18°C for 18 h and 5°C for 6 h, with a 24 h photoperiod (incandescent and fluorescent lamps), and percent germination success (appearance of a radical) was measured after 4 d.

Data analysis

Repeated measures analysis of variance was conducted on the phenological data following von Ende (1993), and was conducted on data from a restricted set of Julian days (JD) representing early growth through full leaf expansion. The exact time span tested differed among years since our sampling dates also varied. Leaf fascicle and female catkin analyses included data from JD 180-202, 165-203, and 171-202 for the years 1992-1994 respectively. Male catkin data had identical start dates, but because male catkins senesce earlier than female catkins, the latest dates included in the analysis were JD 194, 194, 195 for 1992-1004 respectively. After these dates, reductions in sample sizes caused by senescence or damage increase substantially. Because missing data are removed from repeated measures analyses, we wanted as large a data set as possible in order to minimize the Type II error rate. Analyses were conducted for years and sexes separately. The overall effect of warming treatment was tested using univariate repeated measures ANOVA, and the time x warming interaction was examined using the Wilks' lambda test in a multivariate repeated ANOVA. Experimental warming, habitat, and sex were fixed effects in all ANOVAS. Non-repeated measures ANOVAS were conducted for SLA, stem increment, female reproductive success, and RE data. Data examined by analysis of variance met the assumptions of normality and homogeneity of variances. A Mann-Whitney U test was conducted on results of

the field germination trials. Linear regression was used to determine the relationsip between number of flowers and catkin length.

Results

Experimentally warmed plants experienced soil and air temperatures above those recorded for control plants throughout each growing season (Fig. 2.1). Season-long seven-day temperature averages from a data collection system established in an array of OTCs and control plots in an adjacent habitat differed by approximately 1.4°C, and maxima and minima by 2.7 and 0.7°C, respectively (Marion et al. 1993). These temperature enhancements are within the range predicted for the high arctic (Maxwell 1992). 1992 data show generally higher temperatures and greater variability in both OTCs and control plots than subsequent years; the high variability was due to measurement technique. Data from the snow depth sensors and personal observations indicate that snow melt occurred no more than three days earlier in the OTCs than in adjacent control plots within any one habitat. The dry habitat accumulates little snow relative to the wet meadow, occasionally leaving plants exposed to freezing and desiccating air, as indicated by frost damage, an effect not observed in the meadow. An lack of snow cover also contributes to earlier growth in the dry habitat.

In the dry habitat, leaf fascicle lengths were consistently longer on warmed plants (Fig. 2.2). However, with the exception of male willows in 1994, these differences were not statistically significant (Table 2.1). In the dry habitat, differences between warmed and control plants increased, and differences between sexes decreased, from one year to the next (Fig.2.2). There was no effect of warming on leaf fascicle length in the wet meadow, although experimentally warmed male plants exhibited significantly faster fascicle elongation (Table 2.1, Fig. 2.2). In 1993, fascicle elongation occurred significantly more rapidly for warmed male willows than controls in both habitats, indicated by the significant time x warming interactions (Table 2.1). Leaf fascicle lengths tended to be slightly shorter for plants in the wet habitat

than for those in the dry. We observed no differences in the timing of leaf yellowing or senescence among years or between habitats, warming treatments or sexes.

Experimental warming generally had little effect on catkin length (Fig. 2.3). In 1993, however, warmed male willows were significantly (P=0.0184) and nearly significantly (P=0.0706) longer than controls in the wet and dry habitats respectively (Table 2.1).The rate of catkin elongation was significantly faster for warmed females and males in the dry habitat in 1992 and 1993 respectively (Table 2.1). During the first two years, catkins in the wet habitat were slightly shorter than those in the dry, but there were no apparent differences in length between habitats in 1994 (Fig. 2.3). In some years we observed a decrease in catkin length for both sexes as the season progressed, but this was probably caused by dehydration due to senescence and to early abscission processes. In the wet habitat in 1992, the abrupt increase in male catkin length about JD 200 reflects a small number ($\leq$6) of later-developing catkins, at the time when those which flowered early in the season were senescing. As with leaf growth, we observed no differences in the timing of seed release among years or between habitats or warming treatments.

Annual stem growth increments were not significantly affected by experimental warming, although mean values were usually greater for warmed plants (Table 2.2). In 1994, warming had a stronger effect on plants growing in the dry habitat (warming x habitat interaction, P=0.05821). Annual stem growth was significantly greater in the dry habitat than in the wet in each year (Table 2.2). The warming treatment significantly increased specific leaf area only in 1994, and SLA was significantly greater for plants from the wet habitat than the dry in 1993 (Table 2.2).

In 1993, all of the female reproductive variables (total capsules/catkin, filling capsules/catkin, total ovules/capsule, green ovules/capsule) were significantly greater in the control plants than in the warmed (Table 2.3). Plants in the dry habitat had significantly greater values for these same variables than those in the wet habitat (Table 2.3). In 1994, however, mean values for the total

number of capsules/catkin and the number of filling capsules/catkin were greater for warmed willows than for the controls, although the differences were not statistically significant (Table 2.3). Warmed plants had lower mean values for the number of total and green ovules/capsule than the controls, but these differences were also not significant (Table 2.3). The linear relationships between catkin length and the number of staminate or pistillate flowers take the following forms:

pistillate flowers = 1.05 (catkin length) + 20.96

($P<0.0001$; $r^2=0.31$)

staminate flowers = 2.54 (catkin length) + 93.24

($P<0.0001$; $r^2=0.23$)

Long female catkins generally have the same number of flowers per unit length as short catkins, while longer male catkins have roughly twice the number of flowers per unit length.

Reproductive effort for both male and female willows was not affected by experimental warming, habitat, or sex when calculated using leaf biomass only or total aboveground biomass (Table 2.4).

Initial germination rates and first-season survival for 1992 seeds sown in the meadow were significantly higher in the warmed plots than in the controls (Table 2.5). By the second season, mortality had reduced initial survival by approximately half, and there were no differences in survival between warmed and unwarmed plots (Table 2.5). Germination rates for 1993 seeds did not differ between warmed and control plots (Table 2.5). Salix arctica seedlings did not germinate in either the sown plots in the dry habitat, or in the unsown recruitment plots in either habitat. The surface of the tilled plots in the dry habitat were dusty when we arrived in early June of 1993 and 1994, and rapidly became dusty again after precipitation events. No germination was observed after these periods of rain or snowfall during the season. In the wet habitat, seeds did not germinate immediately after sowing in August, even though the soil was moist at that time. This may be an adaptation common in willows to prevent fall mortality (Densmore and Zasada 1983).

Laboratory germination tests of 1992 seeds resulted in similar germination rates for seeds collected from warmed and control plants in each habitat (Table 2.6). Chilling and freezing treatments had no apparent effect on germination rates (Table 2.6). Seeds collected from a number of sites on Ellesmere Island in 1993 exhibited similar germination rates in the laboratory; however, 1993 germination rates were higher than those for the previous year (Table 2.6). Low seed production in OTCs and in the wet meadow limited our ability to test among warming treatments and habitats.

Discussion

Contrary to our expectations, leaf fascicles, catkins, and annual stem increments were rarely lengthened significantly by the experimental warming treatment. Other studies of high arctic species have found enhanced growth when temperature was ameliorated by warming treatments in the range produced by our OTCs (Havstrõm et al. 1993). In low and sub-arctic sites, however, temperature had less of an effect than at higher latitudes (Parsons et al. 1994, Wookey et al. 1993). Arctic species are well adapted to growth in cold environments (Billings 1992), and temperature affects arctic species primarily by limiting the rates at which other resources become available (Kielland and Chapin 1992).

It was less surprising, then, to find evidence of a cumulative effect of warming in the responses of arctic willow. In the dry habitat, the pattern of leaf fascicle and male catkin lengths between warming treatments changed after three years; by the third year, differences between warming treatments were greatly pronounced. Additional evidence is found in the significant increase in specific leaf areas in warmed plants in the third year of this study, and the increase in SLA for warmed plants in the dry habitat between 1993 and 1994. Finally, substantial increases in the number of flowers and fruits in warmed plants were apparent in 1994. Together, these responses provide reasonably good evidence for a real change in plant responses over time.

The mechanism or mechanisms responsible for these effects are uncertain, but undoubtedly involve a whole-plant response (Chapin 1991). In this study, and in the controlled environment study described in Chapter 5, temperature alone had a relatively weak effect on growth and photosynthesis. However, temperature and fertilization together may have substantially stronger, and potentially interactive, effects (Havstrōm et al. 1993, Parsons et al. 1994). Photosynthetic rates in Salix arctica may have increased sufficiently with temperature to supply the carbon resources necessary for additional growth, but this would require that additional nutrient resources were also available. In arctic systems, soil temperature and moisture, as well as substrate quality, strongly influence decomposition and nutrient mineralization (Nadelhoffer et al. 1992), nitrogen fixation (Chapin and Bledsoe 1992), and mycorrhizal availability and function (Kohn and Stasovski 1990). Thus, the three-year impact of our experimental warming treatment on the relatively warm, dry soils of the dry habitat examined in this study may have been sufficient to provide supplemental nutrients to support the increase in growth.

Whether the OTCs have had an effect on soil nutrient mineralization remains to be examined at Alexandra Fiord, but if so, this would help explain the differences between treatments, since Salix arctica appears responsive to nutrient additions (Woodley and Svoboda 1994). Two previous studies involving Salix arctica at Alexandra Fiord found that NPK fertilization treatments increased green biomass in this species, and the effects were greater in dry habitats than in the sedge meadow communities (Henry et al. 1986, Woodley and Svoboda 1994). Leaf area in alpine populations of Salix glauca was enhanced by N fertilization (Bowman and Conant 1994), a response typical of arctic species (Chapin and Shaver 1985). On the other hand, fertilization did not affect phenology in S. arctica (Henry et al. 1986, Woodley and Svoboda 1994), which is consistent with our results.

Female reproductive success was generally lower in the OTCs relative to controls. This effect was not unanticipated, however, since the OTCs themselves restrict pollinator visits to flowers inside the chambers (pers. obs.),

and also reduce the potential for successful wind pollination. In contrast to our observations, Ulf Molau (pers. comm.) found that identical OTCs at ITEX sites in northern Sweden have a positive influence on pollinator visits. Both insect and wind pollination occurs in Salix arctica at Alexandra Fiord (unpubl. data), and seed set in many (if not most) willows is pollen-limited (Fox 1992). Consequently, an unwanted side effect of the OTCs at Alexandra Fiord might be inaccurate estimates of shifts in female reproductive potential induced by pollen limitations.

Our initial expectation was that warming would increase reproductive effort after three years, but RE was not affected by warming, habitat or sex. We observed that willows which flowered heavily one year tended to have fewer catkins the next, and this year to year variation may have influenced our results. This may also indicate that at least one growing season is required to restore the resource capital necessary for re-investment in reproductive structures. Fox and Stevens (1991) found that a reduction in reproductive allocation one year tended to stimulate floral bud development in subsequent years in the sub-arctic willow Salix alexensis.

Other factors which could influence reproductive potential also require further investigation. In stressed or resource-limited environments like the High Arctic, we might anticipate that heavy pollination of one catkin would divert resources from other catkins, thereby reducing overall reproductive potential. This may not be the case, however. Fox (1992) found autonomy of catkins in five Alaskan willow species, and suggested that resources may be committed to reproduction as each catkin develops, and that the catkins themselves (or their subtending leaves on the catkin petioles in S. arctica) may be photosynthetically self-supportive. In an elegant study of reproductive costs, Fox and Stevens (1991) found no reduction in shoot growth associated with reproduction of Salix alexensis. This study is reassuring in that differences in stem growth between willows growing in OTCs and in control plots were probably not influenced by lower reproductive allocation induced by the effect of OTCs on pollinators. Whether demonstrable reproductive costs in the high

arctic willow species we examined, or whether reproductive costs shift with warming and changes in soil nutrient and moisture dynamics, remain to be investigated.

Our baseline data correlating catkin length with flowering potential, coupled with the apparent responsiveness of male catkin length to the warming treatment of a few degrees, suggests that male willows may have the potential to double their pollen production under a changed climate. These observations must be viewed with caution, however. We do not know whether pollen production actually increases with length, or whether the number of pistillate flowers or ovules/capsule might eventually increase with time, particularly in response to improved soil nutrients. An increase in pollen availability would not necessarily result in greater viable seed production, since it appears that total pistillate flower production in females may not increase with warming; viable seed production could increase in response to warming, however. Seedling recruitment into intact tundra is infrequent (Freedman et al. 1994, McGraw and Fetcher 1992). Nevertheless, if male willows in the dry habitat respond more favorably to climate warming than those in the meadow, as indicated by the catkin growth data, they could benefit from a selective advantage if reproduction from seed increases with climate change. Differential fitness such as this would probably lead to shifts in the genetic structure of natural populations and communities under the influence of long-term climate change (Strain 1991, McGraw and Fetcher 1992).

However, the scale at which environmental heterogeneity occurs may help maintain genetic variation (Mitchell-Olds 1992), and may eventually play a role in the extent to which genetic variability changes at Alexandra Fiord. Ironically, willow seed production is currently (and likely to remain) much greater in the dry habitat, but no seed germination occurred there during this study, probably due to low soil moisture (Bell and Bliss 1980). Juxtaposed to this is the relatively low seed production in the meadow, where substantial germination and establishment is more likely to occur in the future. We observed no seedling recruitment in our unsown plots, and observed very few

S. arctica seedlings in disturbed surfaces dating from 1980. Freedman et al. (1982) found relatively numerous Salix arctica seedlings in only one relatively warm, dry plant community at Alexandra Fiord, and no viable seeds in seeds banks excavated from this or any other habitat. Future seedling recruitment of Salix arctica - possibly representing novel genetic variability - will likely depend on the location and extent of soil disturbances or suitable microsites.

Table 2.1. Results of repeated-measures ANOVA for Salix arctica leaf fascicle and catkin elongation in OTCs and control plots in dry and wet habitats, 1992-1994. N=number of samples, P= significance level.

LEAVES		1992		1993		1994	
HABITAT	FACTOR	N	P	N	P	N	P
DRY							
FEMALE	WARMING	60	0.3182	60	0.2434	20	0.3819
	TIME X WARM		0.0944		0.7364		0.9514
MALE	WARMING	58	0.0761	48	0.2596	15	0.0046
	TIME X WARM		0.8099		0.0539		0.5374
WET							
FEMALE	WARMING	57	0.6504	95	0.9991	19	0.4758
	TIME X WARM		0.4351		0.3585		0.3822
MALE	WARMING	60	0.6537	92	0.9908	26	0.4434
	TIME X WARM		0.0484		0.0115		0.0292

CATKINS		1992		1993		1994	
HABITAT	FACTOR	N	P	N	P	N	P
DRY							
FEMALE	WARMING	59	0.1184	30	0.3661	10	0.7525
	TIME X WARM		0.0081		0.4667		0.9277
MALE	WARMING	43	0.2885	43	0.0706	13	0.3694
	TIME X WARM		0.6871		0.0256		0.2718
WET							
FEMALE	WARMING	50	0.5307	20	0.4986	10	0.9715
	TIME X WARM		0.0709		0.2306		0.1017
MALE	WARMING	36	0.1651	21	0.0184	7	0.6418
	TIME X WARM		0.6473		0.5214		0.9795

Table 2.2. Salix arctica annual stem increments (mm) and specific leaf area ($cm^2\ g^{-1}$) means and standard errors. Data are from plants growing in OTCs and control plots, 1992-1993. N=number of stems or leaves examined. Significance levels (P) for ANOVA results shown in right-hand colums for factors of experimental warming, habitat, and warming x habitat interaction.

STEM INCREMENTS	WARMED			CONTROLS			P		
1992	N	MEAN	SE	N	MEAN	SE	WARMING	HABITAT	W x H
DRY	59	15.80	1.54	54	13.43	1.19	0.7244	0.0001	0.0705
WET	59	7.08	0.58	57	8.68	0.79			
1993									
DRY	59	9.46	1.11	54	7.48	0.71	0.1314	0.0007	0.3831
WET	59	5.90	0.83	57	5.37	0.49			
1994									
DRY	22	7.75	1.11	15	5.93	1.21	0.2422	0.0068	0.05821
WET	14	4.23	1.17	17	3.57	0.38			
SPECIFIC LEAF AREAS									
1993									
DRY	9	75.84	2.04	9	79.87	3.89	0.6996	0.0241	0.5258
WET	9	87.60	5.36	9	86.62	3.96			
1994									
DRY	9	95.78	10.97	10	72.71	2.08	0.0152	0.9037	0.2006
WET	10	87.25	4.83	10	79.78	3.38			

Table 2.3. Salix arctica female reproductive success (means and SE) for willows growing in OTCs and control plots in the dry and wet habitats. In 1994, no female catkins were available for analysis from the wet habitat. For total and green ovules per capsule data, n=number of capsules(catkins) examined. Significance levels (P) for ANOVA results shown in right-hand colums for factors of experimental warming, habitat, and warming x habitat interaction.

		WARMED			CONTROLS			P		
		MEAN	SE	N	MEAN	SE	N	WARMING	HABITAT	W x H
TOTAL CAPSULES/CATKIN										
1993	DRY	35.50	3.04	10	46.50	3.63	10	0.0026	0.0051	0.8981
	WET	24.50	3.88	4	36.40	2.24	10			
1994	DRY	86.67	9.81	6	68.00	4.35	6	0.1125		
FILLING CAPSULES/CATKIN										
1993	DRY	9.50	3.77	10	43.00	3.47	10	0.0001	0.0006	0.0309
	WET	2.25	1.44	4	15.10	4.89	10			
1994	DRY	68.67	5.33	6	58.67	5.01	6	0.5273		
TOTAL OVULES/CAPSULE										
1993	DRY	14.70	4.56	30 (10)	35.00	3.29	30 (10)	0.0086	0.0041	0.1903
	WET	6.00	3.20	30 (10)	13.20	4.79	30 (10)			
1994	DRY	11.44	1.20	18 (6)	14.39	0.99	18 (6)	0.0883		
GREEN OVULES/CAPSULE										
1993	DRY	10.90	4.02	30 (10)	27.90	3.41	30 (10)	0.0148	0.0041	0.1007
	WET	5.25	2.73	12 (4)	8.80	2.92	30 (10)			
1994	DRY	7.28	1.71	18 (6)	9.78	2.01	18 (6)	0.3364		

Table 2.4. Results of ANOVA for Salix arctica reproductive effort (RE, g catkin/g leaf, or g catkin/g total aboveground biomass) for male and female willows in OTCs and control plots in the dry and wet habitats after three growing seaons. Three-way interaction was not possible because of zero df caused by lack of catkins on experimentally warmed male plants in the meadow.

	BY LEAF BIOMASS	BY TOTAL ABOVEGROUND BIOMASS
SOURCE	P	P
Warming	0.6202	0.6557
Sex	0.6858	0.4504
Habitat	0.2059	0.5697
Warming x Sex	0.5041	0.2015
Sex x Habitat	0.6667	0.7387
Warming x Habitat	0.3206	0.1763

Table 2.5. Salix arctica field germination results. Data shown are from the wet habitat only since no germination occurred in the dry habitat. WARMED and CONTROL refer to experimental warming treatments after sowing. Seeds tested were collected from dry habitat control plots only. * indicates significant difference (P=0.05) between warmed and control plots, Mann Whitney U test. Decline in % alive indicated increasing mortality over time.

1992 SEEDS	PLOT	WARMED % ALIVE	CONTROL % ALIVE	SIG.
GERMINATION				
19-Jun-93	1	79	58	*
	2	72	54	
	3	79	62	
SURVIVAL				
10-Aug-93	1	46	38	*
	2	63	40	
	3	48	22	
26-Jun-94	1	36	19	ns
	2	57	40	
	3	43	21	
1993 SEEDS				
GERMINATION				
26-Jun-94	1	48	10	ns
	2	22	21	
	3	62	33	

Table 2.6. Salix arctica laboratory germination results from Alexandra Fiord and other locations on Ellesmere Island. Notes: [1] Seeds kept cool, tested at season end. [2] Seeds refrigerated at 2°C for 5 months. [3] Seeds frozen at -2°C for 5 months.

	SEED SOURCE							
	DRY				WET			
	WARMED		CONTROL		WARMED		CONTROL	
1992 SEED YEAR	%	N	%	N	%	N	%	N
Alexandra Fiord	66	100 [1]	74	200 [1]	60	100 [1]	56	100 [1]
			63	300 [2]				
			67	600 [3]				
1993 SEED YEAR								
Alexandra Fiord			86	1652 [1]				
Eastwind Lake			94	358 [1]				
Princess Marie Bay			86	246 [1]			88	134 [1]
Sverdrup Pass			87	608 [1]				
Hotweather Creek			91	675 [1]				

Figure 2.1. Soil (3 cm) and air (10 cm) temperatures in the OTCs and control plots in the dry and wet habitats at Alexandra Fiord, 1992-1994. Lines represent daily mean temperatures; vertical bars represent ± 1 SD.

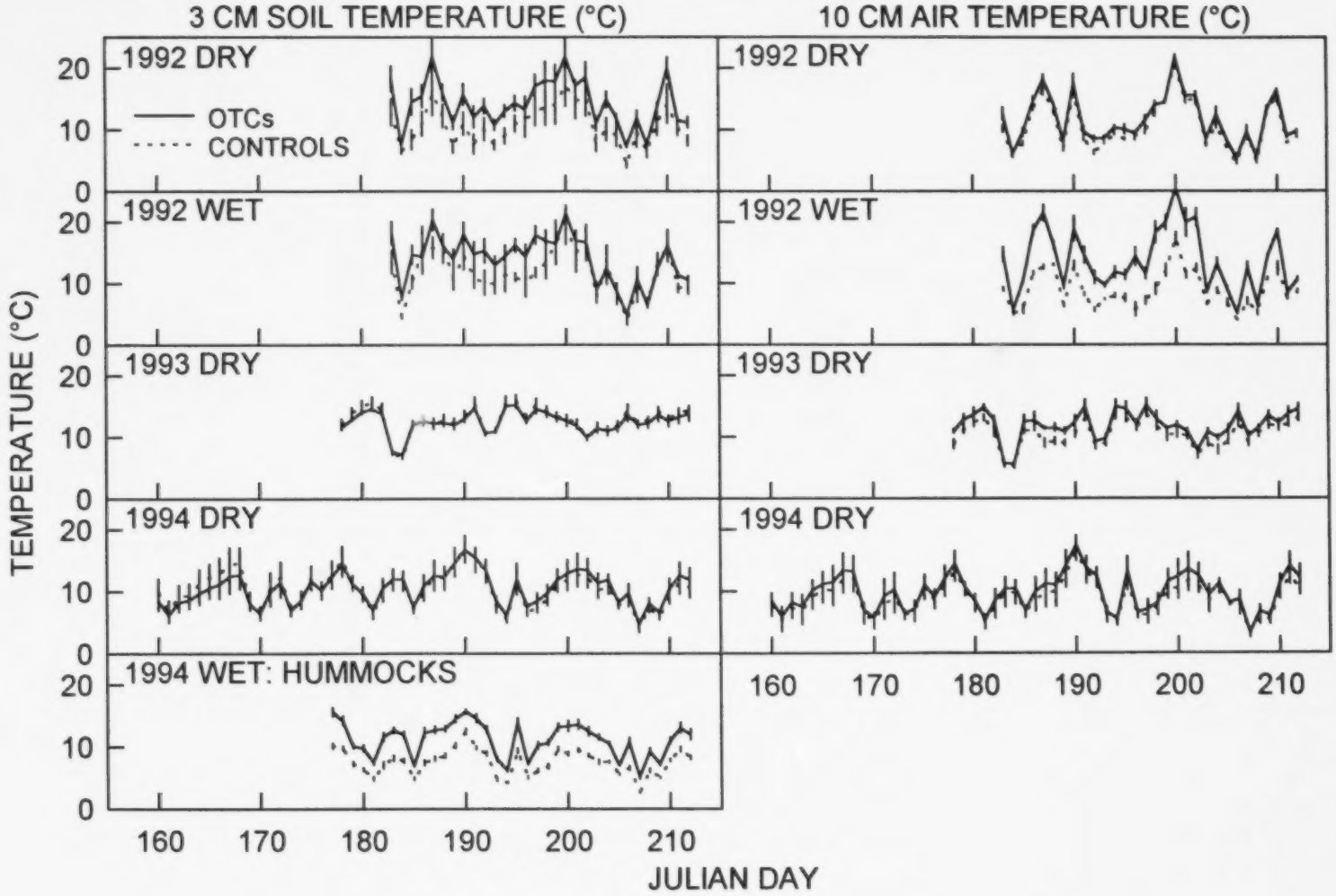


Figure 2.2. Elongation of Salix arctica leaf fascicles for plants growing in OTCs and control plots in the dry and wet habitats, 1992-1994.

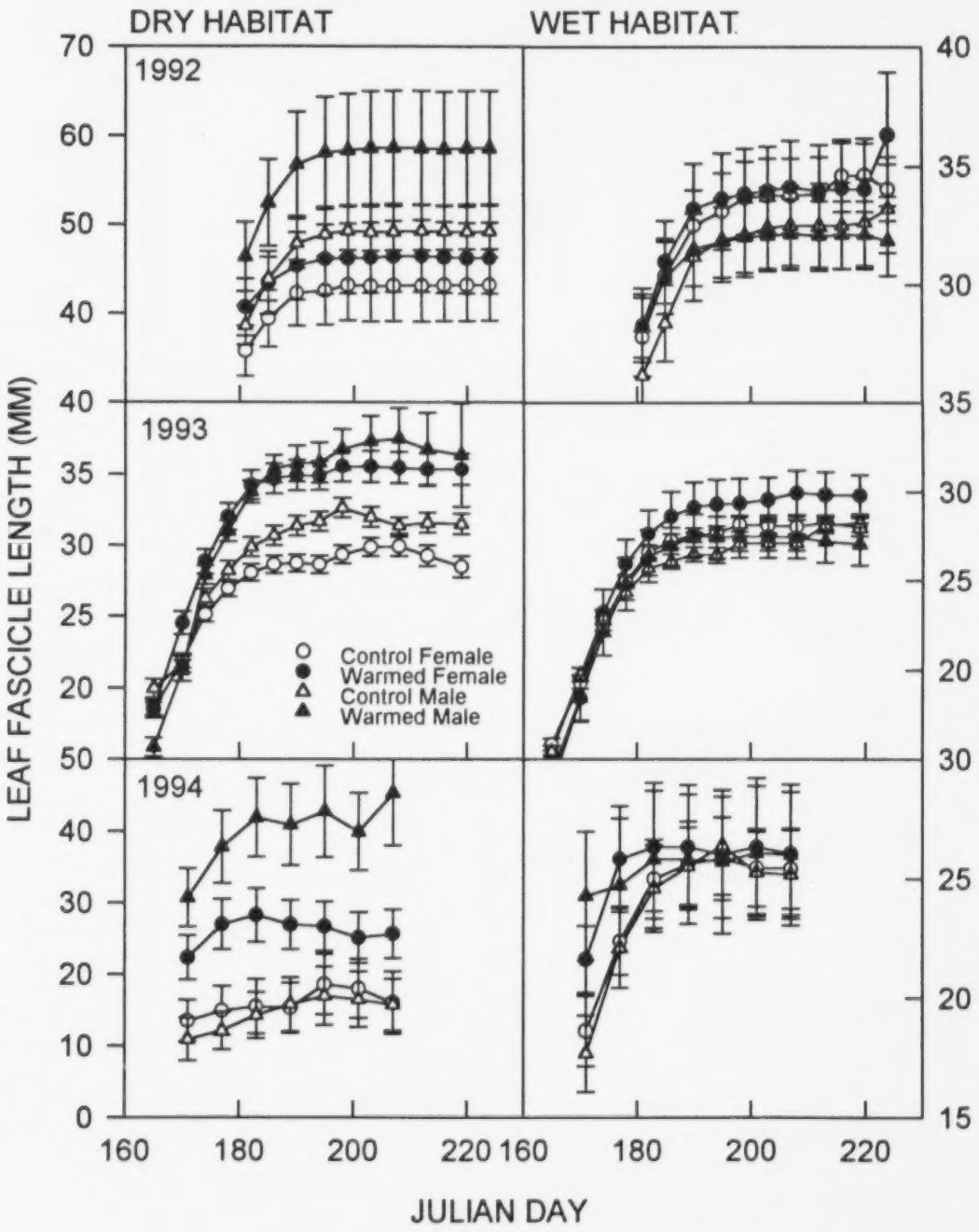
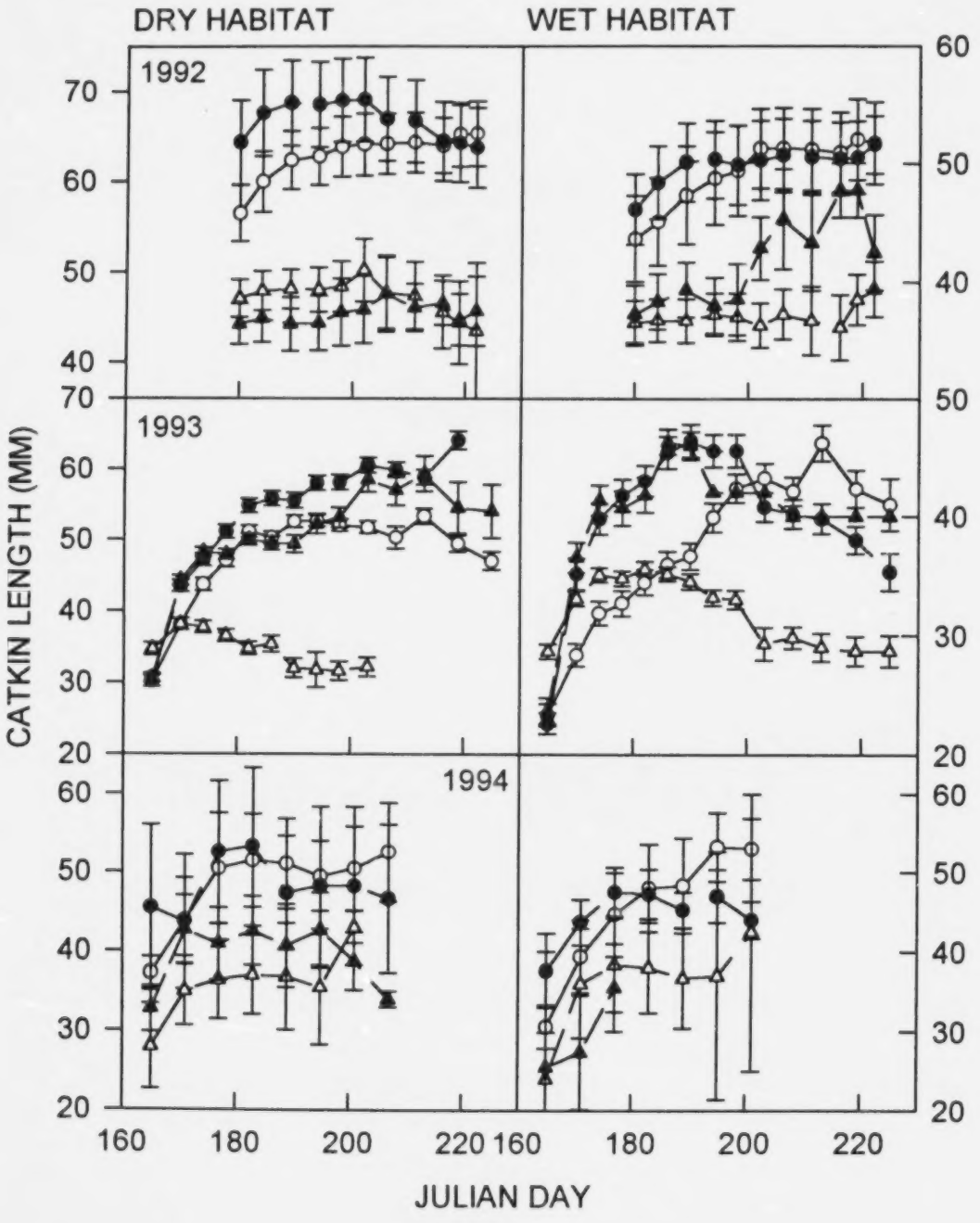


Figure 2.3. Elongation of Salix arctica catkins for plants growing in OTCs and control plots in the dry and wet habitats, 1992-1994. Note varying scales on the vertical axes. Symbols as in Figure 2.2.



References

Bell, K. L., and L. C. Bliss. 1980. Plant reproduction in a high arctic environment. Arctic and Alpine Research **12**:1-10.

Billings, W. D. 1992. Phytogeographic and evolutionary potential of the arctic flora and vegetation in a changing climate. Pages 91-109 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Bowman, W. D., and R. T. Conant. 1994. Shoot growth dynamics and photosynthesis response to increased nitrogen availability in the alpine willow Salix glauca. Oecologia **97**:93-99.

Chapin, D. M., and C. S. Bledsoe. 1992. Nitrogen fixation in arctic plant communities. Pages 301-320 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Chapin, F. S., III. 1991. Integrated responses of plants to stress. BioScience **41**:29-36.

Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology **66**:564-576.

Chapin, F. S., III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver, and J. Svoboda. 1992. Arctic plant physiological ecology in an ecosystem context. Pages 441-451 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Densmore, R., and J. Zasada. 1983. Seed dispersal and dormancy patterns in northern willows: ecological and evolutionary significance. Canadian Journal of Botany **61**:3207-3216.

Fox, J. F. 1992. Pollen limitation of reproductive effort in willows. Oecologia **90**:283-287.

Fox, J. F., and G. C. Stevens. 1991. Costs of reproduction in a willow: experimental responses vs. natural variation. Ecology **72**:1013-1023.

Freedman, B., N. Hill, J. Svoboda, and G. H. R. Henry. 1982. Seed banks and seedling occurrence in a High-Arctic oasis at Alexandra Fiord, Ellesmere Island, Canada. Canadian Journal of Botany **60**:2112-2118.

Havstrõm, M., T. V. Callaghan, and S. Jonasson. 1993. Differential growth responses of Cassiope tetragona, an arctic dwarf-shrub, to enviornmental perturbations among three contrasting high- and subarctic sites. Oikos **66**:389-402.

Henry, G. H. R. 1987. Ecology of sedge meadow communities of a polar desert oasis: Alexandra Fiord, Ellesmere Island, Canada. Ph.D. Dissertation. University of Toronto, Toronto, Canada.

Henry, G. H. R., B. Freedman, and J. Svoboda. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. Canadian Journal of Botany **64**:2502-2507.

Henry, G. H. R., J. Svoboda, and B. Freedman. 1990. Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. Canadian Journal of Botany **68**:2660-2667.

Labine, C. 1994. Meteorology and climatology of the Alexandra Fiord lowland. Pages 23-40 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, ONT.

Kielland, K., and F. S. Chapin III. 1992. Nutrient absorption and accumulation in arctic plants. Pages 321-336 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Kohn, L. M., and E. Stasovski. 1990. The mycorrhizal status of plants at Alexandra Fiord, Ellesmere Island, Canada, a high arctic site. Mycologia **82**:23-35.

Marion, G. M., G. H. R. Henry, P. Molgaard, W. C. Oechel, M. H. Jones, and G. L. Vourlitis. 1993. Open-top devices for manipulating field temperatures in tundra ecosystems. Lunardini,V.J. and S.L. Bowen, eds. Proceedings, Fourth International Symposium on Thermal Engineering and Science for Cold Regions, 28 Sept.-1 Oct. 1993. U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH. (205-210)

Maxwell, B. 1992. Arctic climate: potential for change under global warming. Pages 11-34 *in* F. S. I. I. I. Chapin, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, CA.

McGraw, J. B., and N. Fetcher. 1992. Response of tundra plant populations to climatic change. Pages 359-376 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Mitchell-Olds, T. 1992. Does environmental variation maintain genetic variation? A question of scale. Trends in Ecology and Evolution **7**:397-398.

Molau, U., editor. 1993. The International Tundra Experiment Manual. Danish Polar Center, Copenhagen.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and J. A. Laundre. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology **72**:242-253.

Parsons, A. N., J. M. Welker, P. A. Wookey, M. C. Press, T. V. Callaghan, and J. A. Lee. 1994. Growth responses of four sub-arctic dwarf shrubs to simulated environmental change. Journal of Ecology **82**:307-318.

Porsild, A. E., and W. J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. National Museums of Canada, Ottawa.

Semikhatova, O. A., T. V. Gerasimenko, and T. I. Ivanova. 1992. Photosynthesis, respiration, and growth of plants in the Soviet arctic. Pages 169-192 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Sorensen, T. 1941. Temperature relations and penology of the northeast Greenland flowering plants. Meddelelser om Gronland **125**:1-307.

Strain, B. R. 1991. Possible genetic effects of continually increasing atmospheric CO_2. Pages 237-244 *in* G. E. Taylor, L. F. Pitelka and M. T. Clegg, editors. Ecological genetics and air pollution. Springer-Verlag, New York, NY, USA.

Svoboda, J., and B. Freedman, editors. 1994. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus University Publications, Toronto.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113-137 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York.

Woodley, E. J., and J. Svoboda. 1994. Effects of habitat on variations of phenology an nutrient concentration among four common plant species of the Alexandra Fiord Lowland. Pages 157-176 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, Ontario.

Wookey, P. A., A. N. Parsons, J. M. Welker, J. A. Potter, T. V. Callaghan, J. A. Lee, and M. C. Press. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. Oikos **67**:490-502.

CHAPTER 3

Sex, habitat, and climate warming: diurnal gas exchange responses of a high arctic willow, Salix arctica

Introduction

At present it is unclear what effects climatic changes anticipated for the coming century will have on terrestrial vegetation in the High Arctic. A doubling of CO_2 is expected to increase temperatures approximately 4°C in summer and 10°C in winter (Maxwell 1992). Most species will respond directly to these changes, but indirect effects may also have a strong impact on community structure and function. Many arctic species have substantial phenotypic plasticity, which may help these species adjust successfully to short-term climate changes (McGraw and Fetcher 1992). Several arctic plant species have been shown to have ecotypic variation at various spatial scales (e.g., Mooney and Billings 1961, Shaver et al. 1979), and plasticity can vary among genotypes (Fetcher and Shaver 1990). Less certain, however, is how much variability exists between sexes for dioecious species, and whether the sexes might respond differently to climatic changes.

Several recent studies have demonstrated physiological differences between male and female plants in different habitats and under varying types and degrees of environmental stresses. Gehring and Monson (1994) found that males had consistently higher net photosynthesis than did female Silene latifolia plants when grown under conditions of limited nitrogen and light. Dawson and Ehleringer (1993) identified significant physiological and morphological differences between female and male Acer negundo trees in wet and dry habitats. Finally, Dawson and Bliss (1989a,b) found important differences between male and female Salix arctica both between wet and dry arctic habitats and between arctic and alpine populations. Each of these studies suggested that the differences observed between the sexes could have a genetic basis, and could be the result of differential selective pressures. Extrapolating from these studies and others, we might anticipate that

photosynthesis, growth, reproduction, and, potentially, local survival of individuals of a given species under the climatic and ecosystem changes anticipated over the coming century may be highly dependent upon its sex or the habitat in which it grows, or both.

Few field studies have directly addressed plant responses to predicted climate change. In Alaska, Chapin and Shaver (1985) examined effects of temperature, nutrients, and shade on several tussock and wet tundra species. Tissue and Oechel (1987) examined effects of temperature and CO_2 on photosynthesis and growth of Eriophorum vaginatum. Small-scale ecosystem CO_2 fluxes were examined by Hilbert et al. (1987), Grulke et al. (1990) and Oechel et al. (1992). In Fennoscandia, the effects of temperature, nutrients, and shading were examined in Cassiope tetragona by Havstrõm et al. (1993), and the effects of temperature, precipitation, and nutrients in several other species by Wookey et al. (1993). These studies demonstrate that responses to experimental warming treatments simulating climatic changes vary widely by species, habitats, and the type of experimental warming treatment imposed. None of these studies, however, examined sex-specific responses to climate warming in the Arctic.

By studying diurnal patterns of gas exchange, we can gain fundamental information on plant responses to natural environments (Schulze and Hall 1982). Moreover, examining diurnal gas exchange patterns may be particularly important for detecting effects of climate change in the arctic, for two reasons. First, the different diurnal radiation regime and other growing conditions are likely to produce different diurnal gas exchange responses than found in plants at temperate latitudes. Second, arctic species are generally sensitive to small changes in temperature (Billings 1992), and single spot measurements may not show the response trends to variations in environmental variables that can occur over time.

In this study we examine the effects of two seasons of experimental warming on the gas exchange responses of Salix arctica Pall. at Alexandra Fiord, Ellesmere Island, in the Canadian High Arctic. This species is a major

component of many high arctic plant communities, and changes in performance or abundance under climatic changes could have substantial impacts on arctic ecosystems. Salix arctica is dioecious, and previous research demonstrated sexual differences in water relations and stomatal conductance that were habitat dependent (Dawson and Bliss 1989a,b). Our experiments were designed to address three fundamental questions related to short-term responses to climate change: (i) what type of diurnal gas exchange patterns does Salix arctica exhibit in the High Arctic? (ii) do patterns differ by habitat or sex? and (iii) are they influenced by experimental warming? This research was conducted as part of the International Tundra Experiment (ITEX).

Methods

Species and study site

The prostrate, deciduous, dioecious shrub Salix arctica is common in circumpolar regions and, in North America, is the only willow species present north of 80° latitude (Porsild and Cody 1980). We examined this species on the lowland at Alexandra Fiord, Ellesmere Island (78°53'N, 75°55'W) in the Canadian Arctic Archipelago. This lowland is a polar oasis, with generally warmer temperatures and more soil moisture than polar desert or semi-desert, which results in greater plant cover and productivity. An extensive description of the ecology of the Alexandra Fiord lowland can be found in Svoboda and Freedman (1994). We examined plants in two habitats. One (DRY) is relatively xeric, characterized by minimal snow deposition, early snowmelt, deep early-season active layer, and dry sandy and peaty soils (Muc et al. 1994). Salix arctica is the dominant species in this location. The second habitat (WET) is a wet sedge meadow with relatively later snowmelt, cold soils with a later-developing active layer, and typically with surface water flowing most of the growing season. Willows are an important component in this habitat but are restricted to hummocks (Henry et al. 1990).

Experimental warming chambers

Plants were subjected to passive warming beginning mid-June 1992 using open-top warming chambers (OTC's). OTC's are 1.5 m diameter hexagons, with 0.5 m high sides inclined inwardly at 60° from horizontal, and are made of translucent fiberglass sheets used in greenhouse applications (Sun-Lite HP, Solar Components Corporation, Manchester, NH, USA). See Marion et al. (1993) for construction and performance details for the OTC's. Chambers were placed over a randomly-selected subset of male and female plants in close enough proximity to enclose one plant of each sex within each OTC, but > 30 cm from chamber edges. Control plants were also randomly selected from male and female pairs within approximately 1m of each other. OTC's and control plots have been left in place on a permanent basis.

In 1992, single mid-afternoon measurements of soil (3 cm) and shielded air (10 cm) temperatures were recorded daily in OTCs and control plots in both habitats using thermocouples and a microvoltmeter (N=12: 3 OTCs and 3 control plots in each habitat). In 1993, continuous, year-round micrometerorological measurements were recorded in six OTCs and six control plots using an array of three soil (3 cm) and one shielded air (10 cm) thermocouple/plot and a datalogging system (CR10, multiplexer, and storage module, Campbell Scientific, Logan, UT, USA). Ultrasonic snow depth sensors (Campbell Scientific Canada Corp., Edmonton, AB, Canada) positioned over three OTCs and three control plots continuously recorded snow depths. General climate data for Alexandra Fiord lowland can be found in Appendix A and in Labine (1994).

Gas exchange and water potential measurements

Net assimilation (NA, μmol m^2 sec^{-1}), stomatal conductance (g_s, μmol m^2 sec^{-1}), residual (mesophyll) conductance (g_r, μmol m^2 sec^{-1}), and dark respiration (μmol m^2 sec^{-1}) were measured using a portable, open-system infrared gas analyser (LCA-3, Analytical Development Corporation, Hoddeson, England) and a conifer leaf chamber (PLC(C)). Light was maintained at saturating levels (>1200 μmol m^{-2} sec^{-1}) by using a portable, 12 volt quartz

halogen light (MR-16, Phillips, Sommerset, NJ, USA) affixed to the leaf chamber. During dark respiration measurements, the leaf chamber was placed within an opaque fabric bag. Flow rate was maintained at 150-200 ml min^{-1} and incoming relative humidity at approximately 20%. Calculations for all variables follow von Caemmerer and Farquhar (1981) and Jones (1985), and are expressed on a projected leaf area basis. Leaves from 1992 were dried in the field; a dry weight:leaf area ratio was later calculated using fresh leaves and a LI-COR Model 3100 leaf area meter (Lincoln, NE, USA). In 1993, leaves were frozen and sealed in plastic bags the field and later measured with the same leaf area meter. Leaf water potentials (ψ_L, MPa) were measured in 1993 only. Leaf disks were allowed to equilibrate for a minimum of 30 min before being measured psychometrically (HR33T Dew Point Microvoltmeter and C-52 Sample Chambers, Wescor, Logan, Utah, USA).

Diurnal gas exchange measurements in 1992 were conducted twice on a set of control plants only. Measurements were made every 3 h for a 24 h period beginning 3 July and every 4 h for a 16 h period beginning 8 July. Snowfall prevented completion of the diurnal cycle for the second set of measurements. The same fully-expanded leaf was measured on each of 20 plants, five males and five females in each habitat (DRY, WET), throughout the first 24 h period. A new set of 20 leaves on the same plants was selected for the second diurnal period. Dark respiration was measured on a separate set of leaves, but on the same plants and at the same time as the photosynthesis measurements. These leaves were allowed to equilibrate under opaque shields for >30 min prior to measurements. On July 5 we also made two sets of spot gas exchange measurements (morning and afternoon) on 80 plants in and out of OTC's, including 10 males and 10 females in each of the warming (WARMED, CONTROL) and habitat (DRY, WET) treatment combinations.

In 1993, diurnal gas exchange measurements (NA, g_s, g_r, but not dark respiration) were made on 32 plants, four for each of the warming (WARMED, CONTROL), habitat (DRY, WET), and sex combinations. Measurements were

made on the same fully-expanded leaf every 4 h over a 48 h period beginning 28 June. During each measurement period, leaf water potentials were measured for two males and two females for each of the warming (WARMED, CONTROL) and habitat (DRY, WET) combinations; each plant was therefore measured every other time period. Disks punched from different, fully expanded leaves were used for each measurement. Although we were consistently able to control for approximate leaf age within years, we were not always able to control for shoot type (i.e., reproductive vs. vegetative) due to differing individual phenologies (see Dawson and Bliss 1993).

Data analysis

Repeated-measures analysis of variance was conducted for all diurnal gas exchange variables for each year, following suggestions by von Ende (1993). For 1993 data, we examined the (fixed) effects of warming treatment, habitat, and sex, with time as the repeated factor. Tests for within-subjects effects were examined using univariate analyses, with P values determined using the Huyhn-Feldt correction for sphericity. Data from 1992 diurnal measurements examined (fixed) effects of habitat and sex, with time as the repeated factor, also using the Huyhn-Feldt correction. Between-subjects effects were also calculated during the repeated-measures procedure. Effects of experimental warming, habitat, and sex in 1992 were examined using a univariate ANOVA.

Results

1992 measurements

Air and soil temperatures in and out of OTC's for both years are shown in Figure 3.2. The effect of OTCs on temperature were generally greater in 1992 than 1993.

The time of measurement had a significant effect on all variables for each day (Table 3.1). Because there were no significant effects of sex on either day, we pooled males and females for graphing purposes. In general, NA, g_s, and g_r remained relatively steady throughout the daytime hours (Fig. 3.1). For

both days, however, declines in NA and g_r during late night-early morning measurements corresponded to decreased leaf temperature; bear in mind that the sun is continuously above the horizon at this time of year. For plants in the wet meadow, stomatal conductance increased at these times. For both days, plants in the dry habitat generally exhibited higher values for all diurnal gas exchange variables than plants in the wet meadow (Fig. 3.1, Table 3.1), but differences were more pronounced on the first day. The effect of habitat was only significant for NA and g_r on day 1 (Table 3.1). On the first day, diurnal variation in NA and g_r was more pronounced for plants in the dry (vs. wet) habitat (significant Time x Habitat interaction), and in g_s for plants from the wet meadow on both days. Respiration remained relatively steady throughout the daytime hours, but also decreased with midnight decreases in leaf temperature. Respiration on day 2 was slightly but consistently lower than on day 1. During the night of day 2, 1.5 m air temperature was about 2°C and snow was falling, yet plants still maintained positive NA under ambient light (data not shown).

Mean values for gas exchange variables measured for plants growing in OTCs and control plots are given in Table 3.2. The experimental warming treatment produced no significant effects at the time we measured gas exchange in 1992, three weeks after erecting the chambers (analyses not shown).

1993 measurements

The general pattern of diurnal variation observed in 1992 was verified in 1993 (significant Time and Time x Habitat interaction for all measures, Table 3.3). Late-night declines were again observed in NA and g_r, with trends more pronounced for plants in the dry habitat (Figs. 3.3-3.5). Plants in the wet meadow showed increased g_s at these times. Also, differences in NA and g_r between the habitats were verified (significant Habitat effect, Table 3.3) with plants from the dry habitat having higher values for both variables (Table 3.2). There were no significant differences in diurnal pattern between the sexes, but

males and females did respond differently to experimental warming, and showed significant differences between the habitats (significant effects of Sex, Habitat x Sex, Warming Treatment x Habitat x Sex, Table 3.3).

In the dry habitat, females typically had higher NA, g_s and g_r than males, and these differences were greater for warmed plants (Table 3.2). Although, in general, effects of experimental warming were slight for plants in the dry habitat, there was a trend for females to show higher NA and g_r when warmed, while males showed the opposite (Table 3.2, Figs 3.3-3.5). In the wet meadow, control females had higher NA and g_r than males, but with experimental warming the opposite trend was observed (Table 3.2, Figs. 3.3-3.5). Females in the OTC's had significantly lower NA, g_s and g_r than the control plants, while for males, warming had little effect (Table 3.2, Figs 3.3-3.5). Leaf water potentials were similar for all warming treatment, habitat, and sex combinations (Table 3.2), and although there was substantial variation (range: -0.2 - -2.5 MPa; data not shown), there were no diurnal trends.

Discussion

Photosynthesis in Salix arctica generally followed a diurnal cycle, apparently influenced strongly by effects of air temperature. At this latitude and season, the sun is continuously above the horizon, but there are large diurnal energy fluxes (Henry 1987, Labine 1994) which help drive air temperature cycles and local weather patterns. In general, all gas exchange measurements changed little over time, with the exception of pronounced decreases in NA and g_r, and increases in g_s, associated with declines in temperature. Stomatal conductance and leaf water potential data suggest that water stress may not be very important for limiting photosynthesis, unlike subarctic (Kauhanen 1986) and boreal species (Dang et al. 1991).

In our examination of plants growing in control plots, photosynthesis was strongly dependent upon habitat. Both males and females had higher values of all gas exchange measures in the dry habitat than in the wet meadow

during both years. Sexual differences, however, were significant only in the second year. Female willows generally had significantly higher NA and g_r than males in both the wet and dry habitats; females in the dry habitat also had higher g_s than males, but in the wet meadow this was reversed. The reasons why we detected strong sexual differences among control plants only in the second year are unclear.

Sexual and habitat differences for water relations and stomatal responses had been found in previous work on this species at Truelove Lowland on Devon Island in the Canadian High Arctic. Dawson and Bliss (1989a,b) determined that male plants performed better on the dry raised-beach ridges than did females; conversely, females performed better in wet and mesic meadows examined. Our measurements at Alexandra Fiord were in contrast to their findings. However, in limited measurements made on Salix arctica at Alexandra Fiord in 1984, Todd Dawson (pers. comm.) found results similar to ours. These observations led us to re-examine our assumptions regarding wet and dry habitats.

The wet meadow we examined typically has standing or flowing water in the hollows between hummocks throughout the growing season. Although willow root systems are generally concentrated in the hummocks and tend to be more fibrous than their dry habitat counterparts (pers. obs.), the high water table probably restricts the zone in which roots can function effectively. Cold, anaerobic soil conditions at the level of the base of the hummocks probably limit water and nutrient uptake to those roots above the water table. Some willows have anatomical or physiological adaptations which allow roots to function under anaerobic conditions (Kramer and Kozlowski 1979), but it is unknown whether these adaptations exist in Salix arctica. In contrast, soils in the dry habitat were warmer and well drained, and willows in this habitat typically have extremely long taproot systems (pers. obs.).

On the other hand, the habitat differences in gas exchange responses of Salix arctica we observed may be fundamentally different than those at

Truelove Lowland due to ecotypic differentiation. Dawson and Bliss (1989a,b,) suggested a genetic basis for performance differences within arctic habitats and between arctic and alpine populations of S. arctica, and ecotypic differentiation has been described for other arctic and alpine species at broad (Billings et al. 1971, Fetcher and Shaver 1990) and extremely fine spatial scales (Shaver et al. 1979, 1986, McGraw and Antonovics 1983). Our observations may not necessarily contradict the conclusions of Dawson and Bliss (1989a,b) regarding habitat-dependent sexual differences in physiology in Salix arctica, but do demonstrate that cross-site comparisons may be misleading without independent confirmation. Likewise, the gas exchange responses of S. arctica in the polar oasis environment at Alexandra Fiord should not be extrapolated to willows growing in the polar desert or semi-desert that predominates in the High Arctic.

The effects of experimental warming on Salix arctica were strongly dependent on the sex of the willow and the habitat in which it grew. Warming had no effect on g_s for either sex in the dry habitat, but caused a decrease in NA and g_r in males. In the wet meadow, warming clearly depressed all gas exchange variables in females throughout the 48 h measurement period, and reduced g_s for males. The effects of warming on NA and g_r for males in the wet meadow varied considerably, but showed a trend of higher rates under the higher, steadier air temperatures. It is possible that these differences could be due to sex or habitat dependent phenotypic plasticity or ecotypic differentiation, as observed in other species.

Why the warming treatment had a stronger effect in the wet meadow than the dry habitat is unclear. Both stomatal and non-stomatal controls on photosynthesis seem to be operating, particularly in the wet meadow. Here, both female and male willows have lower g_s in OTC's, but only females showed consistently lower NA. In the dry habitat, experimentally-warmed willows may not have experienced air temperatures or vapor pressure deficits high enough to substantially tax their abilities to acquire soil moisture. In contrast, we

suspect that willows in the wet meadow experienced higher water stress caused by restrictive soil conditions and reduced effective root surface area, as discussed above.

In controlled environment studies with Salix arctica (Chapter 5), we observed no significant differences in gas exchange characteristics between plants from the wet and dry habitats when grown under common conditions. This suggests that differences in plant performance observed under field conditions may be related more to immediate environmental conditions than to inherent differences between populations.

Based on the short-term results reported here, and with unchanged soil moisture regimes, female willows in the wet meadow are likely to have reduced photosynthesis under a warmed environment, with potentially negative impacts on growth or survival. The response of male willows in the wet meadow is more difficult to predict, but they could increase in cover because of their higher NA rates under warmed conditions. Although the responses of males in the dry habitat are not as clear as those of females, it is possible that cover or numbers of males could be diminished. Whether the changes we observed in NA would, in fact, have an impact at the population or community level is unclear without longer-term studies. However, if substantial reductions in numbers of males or females were to occur, highly-skewed sex ratios would result. This could have an important effect on sexual reproduction, since segregation of the sexes would occur over larger spatial scales.

These results do not consider potential effects of increased CO_2 (Chapter 5), which could alter the response to warmer air temperature (Farrar and Williams 1991, Long 1991). Homeostatic adjustments to increased CO_2 have been observed in individual plants (Oechel and Strain 1985, Oberbauer et al. 1986) and at the ecosytem level (Grulke et al. 1990), so that the long-term effects of elevated CO_2 are as yet uncertain. However, heritable response differences to elevated CO_2 have been demonstrated in some species (Wulff and Alexander 1985, Curtis et al. 1994).

Other factors related to climate changes, such as soil water regimes, active layer depth and soil temperature, nutrient mineralization and availability, and so on, are also likely to affect the phenology, growth, and productivity of Salix arctica. For example, Salix arctica responded positively to applications of N and NPK fertilizer in three plant communities at Alexandra Fiord (Henry et al. 1986). Nitrate reductase activity in Salix arctica is low relative to several other arctic species (Atkin et al. 1993), potentially limiting its growth in some communities and soil types.

Table 3.1. Results of ANOVA of gas exchange variables for Salix arctica in control plots only in dry and wet habitats, measured 3-4 and 8-9 July 1992 (N=20 plants measured each day).

		GAS EXCHANGE VARIABLES											
		NET ASSIMILATION			STOMATAL CONDUCTANCE			RESIDUAL CONDUCTANCE			RESPIRATION		
DAY	SOURCE	df	F	P	df	F	P	df	F	P	df	F	P
1	Within-subjects effects												
	Time	6	8.39	0.0001	6	2.61	0.0300	6	9.07	0.0001	6	10.17	0.0001
	Time x Habitat	6	3.44	0.0040	6	5.76	0.0001	6	3.26	0.0058	6	6.58	0.0001
	Time x Sex	6	2.07	0.0639	6	0.86	0.5135	6	2.02	0.0698	6	0.57	0.7530
	Time x Habitat x Sex	6	1.06	0.3919	6	1.24	0.2983	6	1.10	0.3700	6	1.28	0.2739
	Error	96			96			96			64		
	Between-subjects effects												
	Habitat	1	16.86	0.0008	1	1.65	0.2170	1	19.88	0.0004	1	0.07	0.7972
	Sex	1	0.00	0.9952	1	0.02	0.8991	1	0.00	0.9767	1	1.66	0.2153
	Habitat x Sex	1	1.95	0.1813	1	0.00	0.9634	1	2.16	0.1610	1	0.50	0.4877
	Error	16			16			16			16		
2	Within-subjects effects												
	Time	5	57.10	0.0001	4	26.76	0.0001	4	33.82	0.0001	6	6.99	0.0002
	Time x Habitat	5	2.18	0.0740	4	5.58	0.0044	4	2.20	0.0839	6	2.03	0.1112
	Time x Sex	5	2.18	0.0740	4	0.33	0.7665	4	2.04	0.1048	6	0.55	0.6786
	Time x Habitat x Sex	5	1.08	0.3763	4	0.22	0.8454	4	1.22	0.3113	6	1.00	0.4074
	Error	80			64			64			64		
	Between-subjects effects												
	Habitat	1	2.41	0.1403	1	2.63	0.1246	1	2.71	0.1192	1	0.40	0.5374
	Sex	1	0.28	0.6046	1	0.54	0.4743	1	0.57	0.4596	1	1.42	0.2512
	Habitat x Sex	1	0.68	0.4227	1	0.07	0.7934	1	0.58	0.4556	1	0.09	0.7654
	Error	16			16			16			16		

Table 3.2. Mean (± SE) gas exchange values for Salix arctica in OTCs and control plots in dry and wet habitats during 1992 (N=80, not diurnal) and 1993 (N=32, diurnal). NA=net assimilation; g_s=stomatal conductance; g_r=residual conductance; WP=leaf water potential; see text for units..

			HABITAT							
			DRY				WET			
			WARMED		CONTROL		WARMED		CONTROL	
YEAR	VARIABLE		MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE
1992 (NOT DIURNAL)	NA	AM	8.3	0.5	8.9	0.9	6.6	0.4	6.1	0.4
		PM	8.9	1.2	12	2	6.2	0.5	5.5	0.4
	gs	AM	188	15	221	23	120	10	208	48
		PM	572	124	683	178	447	32	400	32
	gr	AM	22.6	1.2	24.4	2.5	18.1	1.1	16.9	1.1
		PM	24	3.3	32.2	5.4	16.8	1.2	14.8	1.2
1993 (DIURNAL)	NA	FEMALE	9.5	0.3	8.8	0.3	5	0.3	7.7	0.5
		MALE	6.7	0.4	7.7	0.2	6.4	0.4	5.4	0.5
	gs	FEMALE	278	15	268	11	189	10	262	16
		MALE	221	8	217	7	231	12	269	15
	gr	FEMALE	26.3	0.9	24.4	0.8	14	0.8	21.7	1.3
		MALE	18.6	1	21.5	0.6	16.9	1.1	15.2	1.3
	WP	FEMALE	-1.1	0.1	-1.2	0.1	-1.2	0.1	-1.2	0.1
		MALE	-1.1	0.1	-1.1	0.1	-1.3	0.1	-1.2	0.1

Table 3.3. Results of repeated-measures ANOVA of diurnal gas exchange variables for Salix arctica in OTCs and control plots in dry and wet habitats, measured 28-30 June 1993 (N=32).

	GAS EXCHANGE VARIABLES								
	NET ASSIMILATION			STOMATAL CONDUCTANCE			RESIDUAL CONDUCTANCE		
SOURCE	df	F	P	df	F	P	df	F	P
Within-subjects effects									
Time	11	3.42	0.0019	11	12.63	0.0001	11	3.19	0.0035
Time x Tmnt	11	0.72	0.6548	11	1.89	0.0676	11	0.76	0.6228
Time x Habitat	11	2.67	0.0120	11	7.53	0.0001	11	2.58	0.0153
Time x Tmnt x Habitat	11	0.94	0.4756	11	1.41	0.1974	11	0.93	0.4847
Time x Sex	11	0.64	0.7196	11	0.74	0.6511	11	.064	0.7199
Time x Tmnt x Sex	11	0.47	0.8592	11	0.54	0.8155	11	0.48	0.8482
Time x Habitat x Sex	11	1.54	0.1553	11	0.85	0.5526	11	1.51	0.1664
Time x Tmnt x Habitat x Sex	11	1.31	0.2492	11	0.88	0.5334	11	1.31	0.2472
Error	264			264			264		
Between-subjects effects									
Tmnt	1	1.14	0.2973	1	2.87	0.1033	1	11.26	0.2722
Habitat	1	14.24	0.0009	1	0.32	0.5782	1	13.59	0.0012
Tmnt x Habitat	1	0.65	0.4276	1	4.65	0.0412	1	0.61	0.4430
Sex	1	5.12	0.0330	1	1.02	0.3230	1	5.07	0.0337
Tmnt x Sex	1	0.52	0.4758	1	0.22	0.6434	1	0.53	0.4741
Habitat x Sex	1	1.25	.02740	1	7.26	0.0127	1	1.23	0.2792
Tmnt x Habitat x Sex	1	5.14	0.0327	1	0.51	0.4832	1	5.07	0.0338
Error	24			24			24		

Figure 3.1. Gas exchange variables (means ± SE) for Salix arctica measured 3-4 July and 8-9 July 1992. NA = net assimilation; g_s = stomatal conductance; g_r = residual conductance. Open circles are male and female plants in the dry habitat; closed circles are male and female plants in the wet meadow.

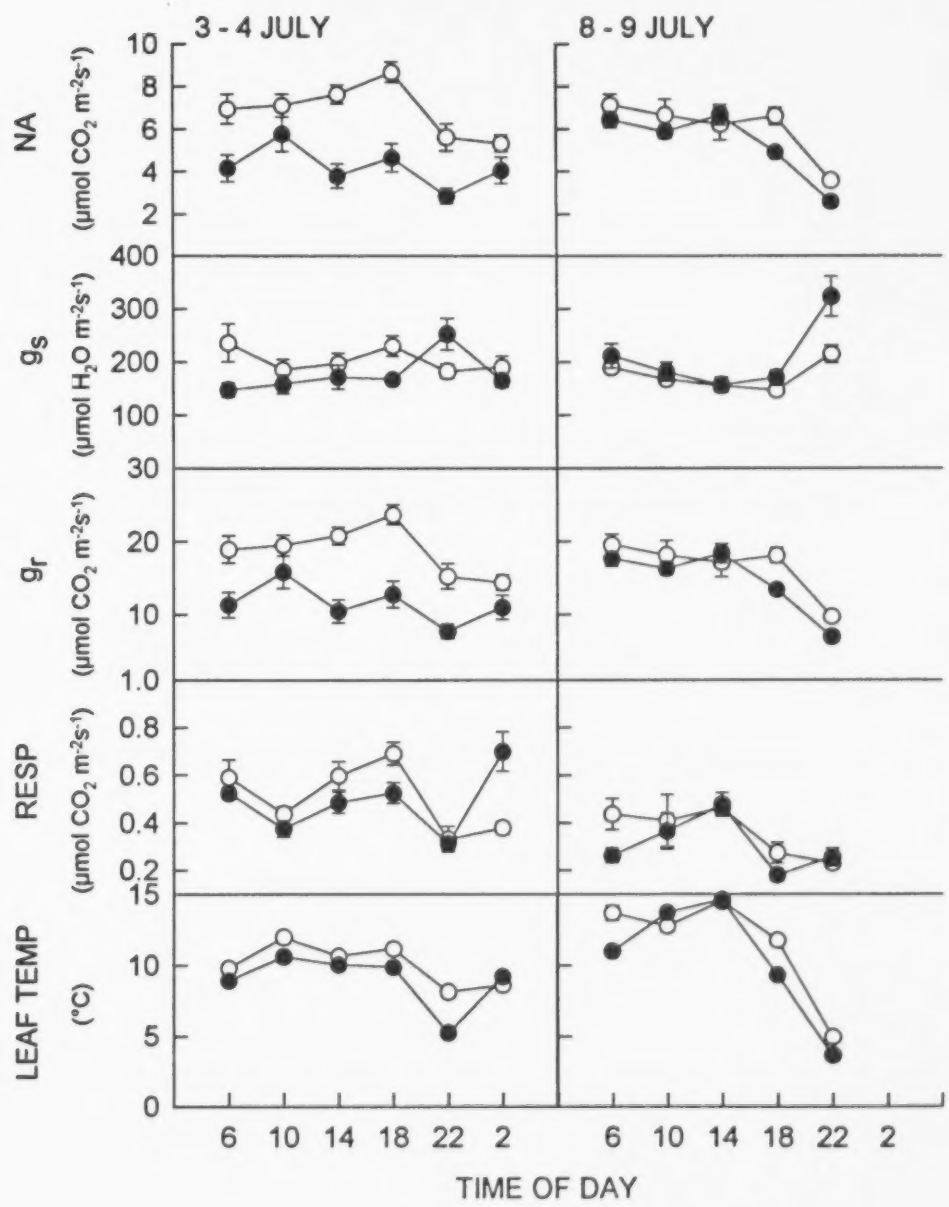


Figure 3.2. Soil (3 cm) and air (10 cm) temperatures in OTCs and control plots in the dry and wet habitats at Alexandra Fiord in 1992 and 1993. Lines represent daily mean temperatures; vertical bars represent ± 1 SD.

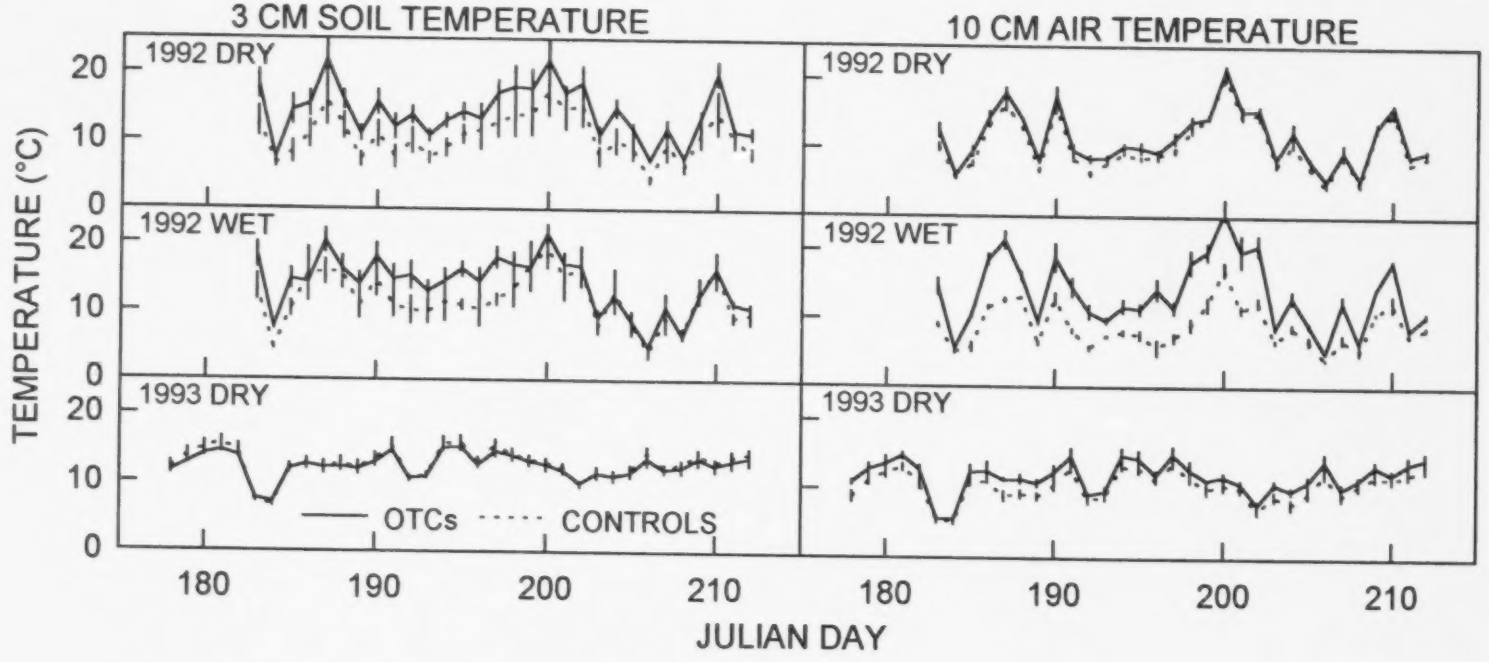


Figure 3.3. Net assimilation (NA) for Salix arctica in OTCs and control plots in the dry and wet habitats, measured 28-30 June 1993; data are means (± SE). Leaf temperatures are means for both sexes in both experimental treatments; error bars not visible.

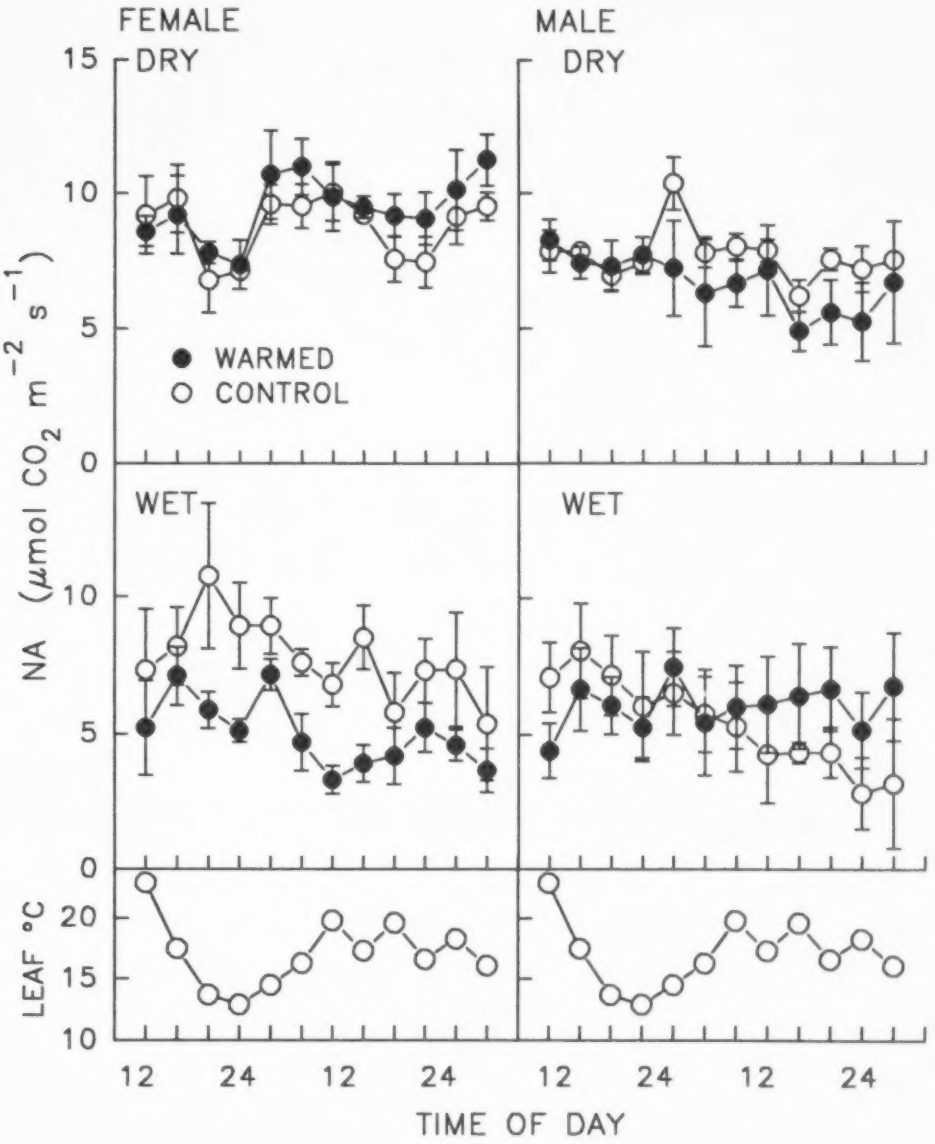


Figure 3.4. Stomatal conductance (g_s) for Salix arctica in OTCs and control plots in the dry and wet habitats, measured 28-30 June 1993. Data are means (± SE).

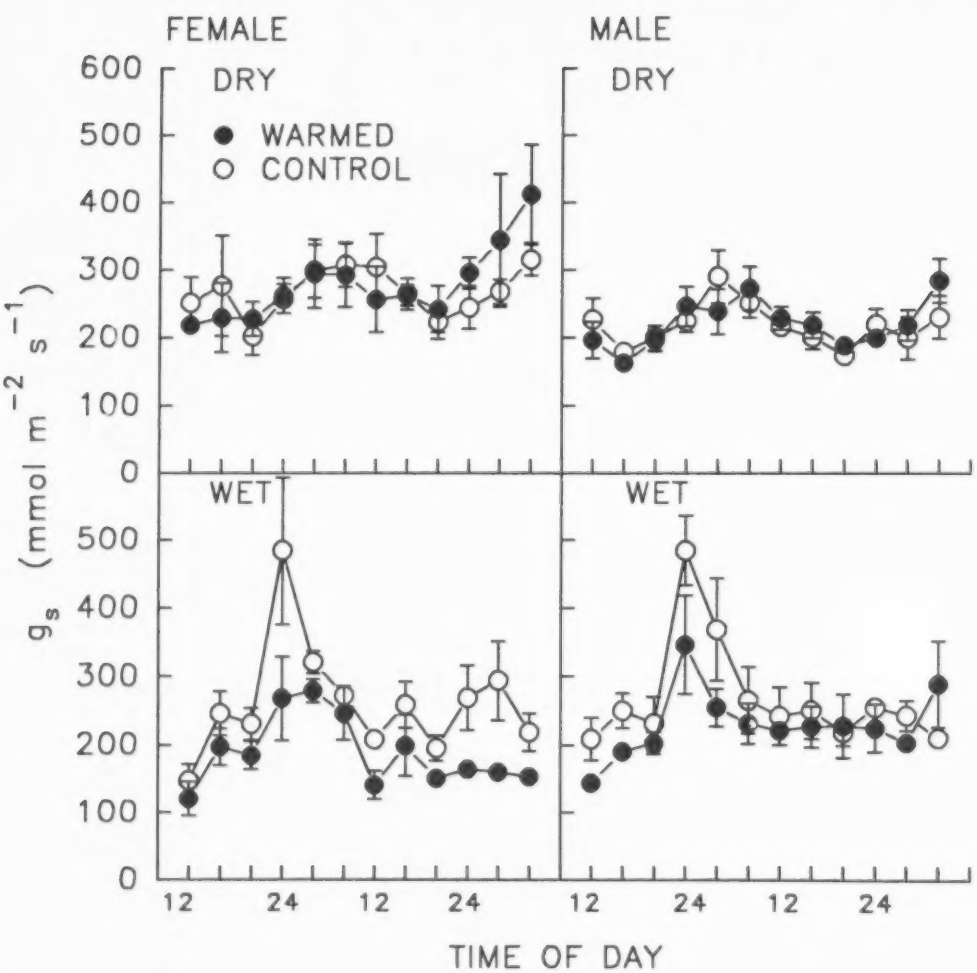
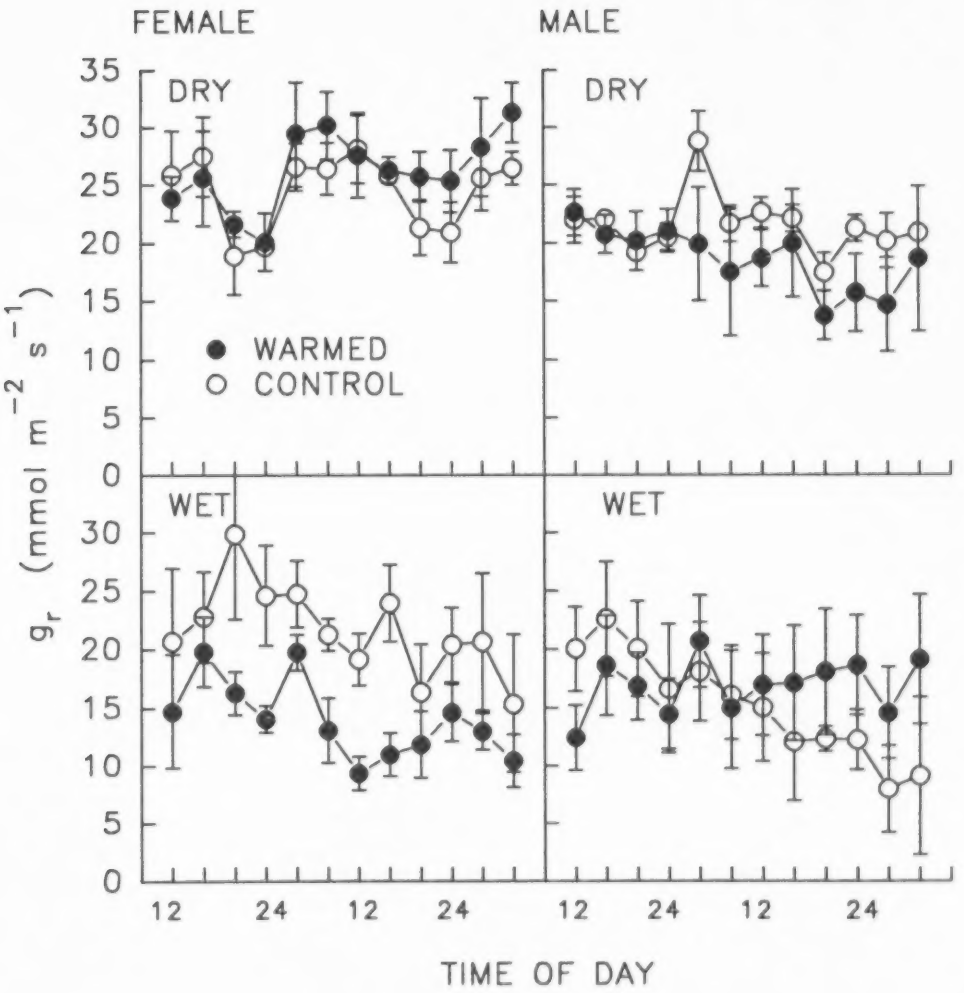


Figure 3.5. Residual conductance (g_r) for Salix arctica in OTCs and control plots in the dry and wet habitats, measured 28-30 June 1993. Data are means (± SE).



References

Atkin, O. K., R. Villar, and W. R. Cummins. 1993. The ability of several high arctic plant species to utilize nitrogen under field conditions. Oecologia **96**:239-245.

Billings, W. D. 1992. Phytogeographic and evolutionary potential of the arctic flora and vegetation in a changing climate. Pages 91-109 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Billings, W. D., P. J. Godfrey, B. F. Chabot, and D. P. Bourque. 1971. Metabolic acclimation to temperature in arctic and alpine ecotypes of Oxyria digyna. Arctic and Alpine Research **3**:277-289.

Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology **66**:564-576.

Curtis, P. S., A. A. Snow, and A. S. Miller. 1994. Genotype-specific effects of elevated CO_2 on fecundity in wild radish (Raphanus raphanistrum). Oecologia **97**:100-105.

Dang, Q. L., V. J. Lieffers, R. L. Rothwell, and S. E. Macdonald. 1991. Diurnal variation and interrelations of ecophysiological parameters in three peatland woody species under different weather and soil moisture conditions. Oecologia **88**:317-324.

Dawson, T. E., and L. C. Bliss. 1989a. Intraspecific variation in the water relations of Salix arctica, an arctic-alpine dwarf willow. Oecologia **79**:322-331.

---. 1989b. Patterns of water use and the tissue water relations in the dioecious shrub, Salix arctica: the physiological basis for habitat partitioning between the sexes. Oecologia **79**:332-343.

---. 1993. Plants as mosaics: leaf-, ramet-, and gender-level variation in the physiology of the dwarf willow, Salix arctica. Functional Ecology **7**:293-304.

Dawson, T. E., and J. R. Ehleringer. 1993. Gender-specific physiology, carbon isotope discrimination, and habitat distribution in boxelder, Acer negundo. Ecology **74**:798-815.

Farrar, J. F., and M. L. Williams. 1991. The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. Plant, Cell and Environment **14**:819-830.

Fetcher, N., and G. R. Shaver. 1990. Environmental sensitivity of ecotypes as a potential influence on primary productivity. The American Naturalist **136**:126-131.

Gehring, J. L., and R. K. Monson. 1994. Sexual differences in gas exchange and response to environmental stress in dioecious Silene latifolia (Caryophyllaceae). American Journal of Botany **81**:166-174.

Grulke, N. E., G. H. Riechers, W. C. Oechel, U. Hjelm, and C. Jaeger. 1990. Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. Oecologia **83**:485-494.

Havstrõm, M., T. V. Callaghan, and S. Jonasson. 1993. Differential growth responses of Cassiope tetragona, an arctic dwarf-shrub, to enviornmental perturbations among three contrasting high- and subarctic sites. Oikos **66**:389-402.

Henry, G. H. R. 1987. Ecology of sedge meadow communities of a polar desert oasis: Alexandra Fiord, Ellesmere Island, Canada. Ph.D. Dissertation. University of Toronto, Toronto, Canada.

Henry, G. H. R., B. Freedman, and J. Svoboda. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. Canadian Journal of Botany **64**:2502-2507.

Henry, G. H., J. Svoboda, and B. Freedman. 1990. Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. Canadian Journal of Botany **68**:2660-2667.

Hilbert, D. W., T. I. Prudhomme, and W. C. Oechel. 1987. Response of tussock tundra to elevated carbon dioxide regimes: analysis of ecosystem CO_2 flux through nonlinear modeling. Oecologia **72**:466-472.

Jones, H. G. 1985. Partitioning stomatal and non-stomatal limitations to photosynthesis. Plant, Cell and Environment **8**:95-104.

Kauhanen, H. 1986. Stomatal resistance, photosynthesis and water relations in mountain birch in the subarctic. Tree Physiology **2**:123-130.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, Orlando.

Labine, C. 1994. Meteorology and climatology of the Alexandra Fiord lowland. Pages 23-40 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, ONT.

Long, S. P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO2 concentrations: has its importance been underestimated? Plant, Cell and Environment **14**:729-739.

Marion, G. M., G. H. R. Henry, P. Molgaard, W. C. Oechel, M. H. Jones, and G. L. Vourlitis. 1993. Open-top devices for manipulating field temperatures in tundra ecosystems. Lunardini,V.J. and S.L. Bowen, eds. Proceedings, Fourth International Symposium on Thermal Engineering and Science for Cold Regions, 28 Sept.-1 Oct. 1993. U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH. (205-210)

Maxwell, B. 1992. Arctic climate: potential for change under global warming. Pages 11-34 *in* F. S. I. I. I. Chapin, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, CA.

McGraw, J. B., and J. Antonovics. 1983. Experimental ecology of Dryas octopetala ecotypes. I. Ecotypic differentiation and life-cycles stages of selection. Journal of Ecology **71**:879-897.

McGraw, J. B., and N. Fetcher. 1992. Response of tundra plant populations to climatic change. Pages 359-376 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Mooney, H. A., and W. D. Billings. 1961. Comparative physiological ecology of arctic and alpine populations of Oxyria digyna. Ecological Monographs **31**:1-29.

Muc, M., J. Svoboda, and B. Freedman. 1994. Soils of an extensively vegetated polar desert oasis, Alexandra Fiord, Ellesmere Island. Pages 41-50 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus University Publications, Toronto.

Oberbauer, S. F., N. Sionit, S. J. Hastings, and W. C. Oechel. 1986. Effects of CO2 enrichment and nutrition on growth, photosynthesis, and nutrient concentration of Alaskan tundra plant species. Canadian Journal of Botany **64**:2993-2998.

Oechel, W. C., and B. R. Strain. 1985. Native species responses to increased atmospheric carbon dioxide concentration. Pages 117-154 *in* B. R. Strain and J. D. Cure, editors. Direct effects of increasing carbon dioxide on vegetation. U.S. Dept. of Energy, Washington, D.C.

Oechel, W. C., G. Riechers, W. T. Lawrence, T. I. Prudhomme, N. Grulke, and S. J. Hastings. 1992. 'CO_2LT' an automated, null-balance system for studying the effects of elevated CO_2 and global climate change on unmanaged ecosystems. Functional Ecology **6**:86-100.

Porsild, A. E., and W. J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. National Museums of Canada, Ottawa.

Schulze, E. D., and A. E. Hall. 1982. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. Pages 181-230 *in* O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler, editors. Physiological plant ecology II. (Encyclopedia of plant physiology. Volume NS vol 12 B). Springer, Berlin Heidelberg New York.

Shaver, G. R., F. S. Chapin III, and W. D. Billings. 1979. Ecotypic differentiation in Carex aquatilis on ice-wedge polygons in the Alaskan coastal tundra. Journal of Ecology **67**:1025-1045.

Shaver, G. R., N. Fetcher, and F. S. Chapin III. 1986. Growth and flowering in Eriophorum vaginatum: annual and latitudinal variation. Ecology **67**:1524-1535.

Svoboda, J., and B. Freedman, editors. 1994. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus University Publications, Toronto.

Tissue, D. T., and W. C. Oechel. 1987. Response of Eriophorum vaginatum to elevated CO2 and temperature in the Alaskan tussock tundra. Ecology **68**:401-410.

von Caemmerer, S., and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta **153**:376-387.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113-137 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York.

Wookey, P. A., A. N. Parsons, J. M. Welker, J. A. Potter, T. V. Callaghan, J. A. Lee, and M. C. Press. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. Oikos **67**:490-502.

Wulff, R. D., and H. M. Alexander. 1985. Intraspecific variation in the response to CO_2 enrichment in seeds and seedlings of Plantago lanceolata L. Oecologia **66**:458-460.

CHAPTER 4

Diurnal gas exchange responses of high arctic sedges to experimental warming at Alexandra Fiord, Ellesmere Island

Introduction

The impact of predicted climatic changes on arctic ecosystems over the coming century may be pronounced. An increase in summer temperature of up to 5°C, caused by a doubling of atmospheric CO_2 and increases in other radiatively active gases (Maxwell 1992), is likely to increase active layer depth, soil decomposition, and nutrient availability, among other changes (Chapin et al. 1992). Effects of the current warming trend may already be apparent. Recent ecosystem-level investigations have determined that tussock and wet sedge tundra are now sources, rather than sinks, of atmospheric CO_2 (Oechel and Vourlitis 1994). Because sedge-dominated communities are highly productive compared to other arctic ecosystems (Wielgolaski et al. 1981, Henry et al. 1990, Muc et al. 1994a), and because of their value for tundra grazers (Henry et al. 1986a, Henry and Svoboda 1994), it is important to understand how they might respond to future environments.

Studies have shown that sedge biomass and photosynthesis are enhanced more by nutrient additions than by elevated temperature (Chapin and Shaver 1985, Shaver et al. 1986a, Henry 1987), or by a doubling of atmospheric CO_2 (Oberbauer et al. 1986, Tissue and Oechel 1987). Others have shown that sedge flowering, growth, and nutrient dynamics are strongly influenced by the plant communities in which they grow (Shaver et al. 1979, Shaver et al. 1986b, McGraw and Fetcher 1992). The fine spatial scale (< 1 m) at which ecotypic differentiation can apparently influence plant performance (for example, nutrient uptake and metabolism, Shaver et al. 1979), may ultimately be more important ecologically than broader latitudinal variation. Fetcher and Shaver (1990) suggest that ecotypes from colder habitats may be less able to respond to temperature amelioration brought about by climatic changes than those from warmer areas, and this could reflect an inability to

respond directly to temperature, or to factors controlled by temperature, such as growing season length.

The wet and mesic sedge meadows at Alexandra Fiord on Ellesmere Island in the Canadian High Arctic have not been significantly grazed by muskox or snow geese for more than 150 y (Henry et al. 1990), and have a well-developed hummock-hollow microtopography. Snowmelt in the hollows is later than on the hummocks, and runoff from snow and ice at higher elevations can strongly influence active layer depth and soil moisture. We wanted to determine whether these microsites had an influence on sedge photosynthesis, and whether experimental warming, simulating climatic changes, altered this effect. We examined diurnal gas exchange patterns in order to better determine the effects of warming and microsite; spot measurements may not reveal variability influenced by frequent variations in weather inherent in the High Arctic. Previously, the only other field gas exchange measurements conducted in the High Arctic were made on whole Carex stans shoots at Truelove Lowland on Devon Island during the International Biological Program (Mayo et al. 1977), although Tieszen (1975) made similar measurements in arctic Alaska. Our work examined short-term responses to experimental warming during the second year of a long-term field experiment, and was conducted as part of the International Tundra Experiment (ITEX).

Methods

Study site and species

This study was conducted at Alexandra Fiord, Ellesmere Island (78°53'N, 75°55'W) in the Canadian Arctic Archipelago during late June and early July of 1992 and 1993. The lowland at Alexandra Fiord is a polar oasis, with generally warmer temperatures and more soil moisture than polar desert or semi-desert environments, which results in generally greater plant cover and productivity. An extensive description of the ecology of the Alexandra Fiord lowland can be found in Svoboda and Freedman (1994). We examined three sedge species - Carex aquatilis stans, Eriophorum angustifolium triste, and Carex

membranacea - in a sedge-dominated community with organic-rich soil (Muc et al. 1994b). Microtopography of the meadow consisted of elevated (10-30 cm) hummocks alternating with hollows with saturated soils or surface water from glacial runoff. The hummocks at Alexandra Fiord are dissimilar in structure and composition to the tussock tundra found, for example, in northern Alaska (Fetcher and Shaver 1982, Henry et al. 1990). There, tussocks are generally more restricted in basal area, and typically have more dwarf shrub growth than the hummocks at Alexandra Fiord.

Experimental warming chambers

Plants were subjected to passive warming beginning mid-June 1992 using open-top warming chambers (OTC's). OTC's are 1.5 m diameter hexagons, with 0.5 m high sides inclined inwardly 60° from horizontal, and are made of translucent fiberglass sheets used in greenhouse applications (Sun-Lite HP, Solar Components Corporation, Manchester, NH, USA). See Marion et al. (1993) for construction and performance details. Chambers were situated to enclose one or more entire hummocks and substantial hollow areas, and to include many individuals of the species of interest. Control plots were located nearby. In 1992, single daily measurements of soil (3 cm) temperatures were recorded on hummocks in OTC's and control plots using thermocouples and a microvoltmeter. In 1994, soil (3 cm) temperatures were continuously recorded on hummocks and in hollows in three OTC's and control plots using an array of thermistors and datalogging systems (Pocketloggers, Pace Scientific, Charlotte, NC, USA). Data recording devices were unavailable during 1993. General climate data for Alexandra Fiord lowland can be found in Appendix A and in Labine (1994).

Gas exchange and water potential measurements

Net assimilation (NA, $\mu mol\ m^2\ sec^{-1}$), stomatal conductance (g_s, $\mu mol\ m^2\ sec^{-1}$), and residual (mesophyll) conductance (g_r, $\mu mol\ m^2\ sec^{-1}$) were measured using a portable, open-system infrared gas analyser (LCA-3, Analytical Development Corporation, Hoddeson, England) and either a PLC(C) (1992) or a PLC3(B) (1993) leaf chamber. Light was maintained at saturating levels (>1200

μmol m^{-2} sec^{-1}) by using a portable, 12 volt quartz halogen light (MR-16, Phillips, Sommerset, NJ, USA) affixed to the leaf chamber. Except during cloudy weather, natural light can be saturating during the middle of the Arctic night at these latitudes. Flow rate was maintained at 150 ml min^{-1} and incoming relative humidity at approximately 20%. Calculations for all variables follow von Caemmerer and Farquhar (1981) and Jones (1985), and are expressed on a projected leaf area basis. Leaf temperature was equated with air temperature in the leaf chamber. Leaves from 1992 were cut, pressed and sealed in plastic bags in the field and later measured in the lab using a LI-COR Model 3100 leaf area meter (Lincoln, NE, USA). In 1993, leaf lengths were standardized (2.5 cm) by leaf chamber size; leaf areas were then calculated geometrically from measured leaf widths.

Diurnal gas exchange measurements in 1992 were conducted only under control conditions on 36 plants, 12 shoots of each species, six on hummocks and six in hollows. The species examined were Carex aquatilis stans, Carex membranacea, and Eriophorum angustifolium triste. Measurements were made every 4 h for a 24 h period on 7-8 July. For each shoot, the same fully-expanded leaf was measured for the entire 24 h period. Measurements for a second 24 h period was interrupted by equipment failure.

In 1993, diurnal gas exchange measurements were made on Carex stans and Eriophorum triste in experimentally warmed and control plots; Carex membranacea was not measured. Measurements were made every 4 h for a 48 h period on 4-6 July. A total of 40 measurements were made at each time period (2 species x 2 positions x 2 warming treatments x 5 reps). Because high water levels in the hollows in 1993 made *in situ* measurements difficult or impossible, leaves were cut and placed in the leaf chamber within 1 min, and measurements were completed within 3 min. Extensive preliminary trials indicated no differences in gas exchange measurements between cut leaves and leaves measured *in situ*. Because of this destructive sampling, we were unable to measure the same shoot consecutively, and sampled a number of shoots

within each plot. Leaf water potentials (ψ_L, MPa) were measured psychometrically on a small circular disk cut from each leaf prior to gas exchange measurements; the disks were allowed to equilibrate 30 minutes prior to measurement (HR33T Dew Point Microvoltmeter and C-52 Sample Chambers, Wescor, Logan, Utah, USA).

Data analysis

Repeated-measures univariate analysis of variance was conducted for 1992 diurnal gas exchange variables, following suggestions by von Ende (1993). Fixed effects were position (hummock or hollow), with time as the repeated factor; P values were determined using the Huyn-Feldt correction for sphericity. For 1993 data, repeated measures analysis could not be used since each measurement was conducted on a different leaf, and a univariate analysis of variance was conducted including time as a non-repeated factor. Fixed effects were position, warming treatment, and time.

Results

Effect of experimental warming chambers

On the hummocks, experimental warming substantially increased soil temperatures above those recorded for control plants throughout most of each growing season (Fig. 4.1). In the hollows, soil temperatures were lower than those on the hummocks, and the OTCs had no effect. Data from 1992 show generally higher temperatures and greater variability in both OTCs and control plots than in 1994; high variability may be due to measurement error associated with technique. Personal observations and data from snow depth sensors in other habitats (Chapter 2) indicate that snow melt occurred no more than three days earlier in the OTCs than in the control plots.

1992 gas exchange measurements

All gas exchange variables showed significant diurnal variation (significant effect of time, Table 4.1). Net assimilation and g_r generally followed diurnal leaf temperatures, with an increase in the early morning hours and a gradual decline after midday (Figure 4.2). Stomatal conductance also increased

in the early morning hours, but then remained level for most of the day, and increased as leaf temperatures began to cool (Fig. 4.2). All three species exhibited similar diurnal trends for both microsites (Table 4.1). Generally, Carex membranacea had the highest values for NA and g_r, followed by Carex stans and Eriophorum triste. For Carex membranacea and Eriophorum triste, NA and g_r were, overall, significantly higher in hollows than on hummocks. There were no significant differences in g_s between microsites for any species.

1993 gas exchange measurements

As in 1992, there was significant diurnal variation for gas exchange variables for both Carex stans and Eriophorum triste (Table 4.2), and NA and g_r generally followed leaf temperature fluctuations, particularly for control plants (Figs 4.3, 4.4, 4.6). Stomatal conductance in both species was not well correlated with leaf temperature, but, as in 1992, g_s increased with the midnight measurements, when temperature was lowest (Fig. 4.5). There was no discernible diurnal pattern of variation in leaf water potential (Fig. 4.6). As in 1992, Eriophorum triste plants generally exhibited lower values for all gas exchange variables than did Carex stans. There were significant effects of microsite position on all gas exchange variables for Carex stans, with plants growing in hollows having significantly greater values than those growing on hummocks.

Experimental warming had a significant effect on NA and g_r for Eriophorum triste (Table 4.2). Under experimental warming, Eriophorum triste plants exhibited lower NA and g_r than controls (Figs 4.3, 4.4), and this trend held for both microsites throughout the 48 h period (no significant time x warming or warming x position interactions, Table 4.2). In Carex stans, warmed plants had significantly higher NA and g_r than control plants on the hummocks (significant warming x position interaction, Table 4.2), but generally lower values than controls in the hollows (Figs 4.3, 4.4). Although g_s tended to be lower in warmed Carex stans in the hollows, the effect was not significant, and g_s did not differ between warming treatments on the hummocks (Fig. 4.5).

Leaf water potentials could not be related to warming, position, or time for either species, although there was a significant position x time interaction for Eriophorum triste (Table 4.3). In general, Ψ_L seemed to follow leaf temperature trends more closely in plants in the hollows.

Discussion

Rather than a mid-afternoon depression of NA and g_s, as reported for boreal or temperate species (Dang et al. 1991, Beadle et al. 1985), all three sedge species growing in control plots exhibited diurnal photosynthesis trends that generally followed air temperatures. Carex membranacea had slightly higher NA than Carex stans and Eriophorum triste, respectively. The effect of microsite was slightly stronger in 1992 than in 1993, and, although the reasons are unclear, could be the result of substantial differences in weather during the two summers. Climate has been shown to account for much of the variability in seasonal biomass production in alpine tundra (Walker et al. 1994). In Alaskan tussock tundra, however, community productivity is relatively stable from year to year, although production of individual species depends more strongly on annual climate variability (Chapin and Shaver 1985; but see Parsons et al. 1994 regarding European tundra). Confounding our results is the observation that values for all gas exchange variables in 1993 were approximately one-fourth that measured in 1992. The cause of these differences is unclear, but does not appear to be related to differences in methodologies; our trials in 1993 found no measurable difference between cut and uncut sedges.

Diurnal photosynthesis patterns similar to those found in the sedges were observed in Salix arctica at Alexandra Fiord (Chapter 3). Our results indicate a correlation between gas exchange and temperature, which contrasts with those of Mayo et al. (1977) for Carex stans on Devon Island, who found a marked diurnal pattern for NA correlated with the diurnal trend in solar radiation, rather than leaf temperature. At Alexandra Fiord, Henry (1987)

found that air temperature was strongly correlated with diurnal radiation budgets, but can vary substantially (Labine 1994). In this study, leaf water potentials did not follow temperature or diurnal insolation patterns, but water stress has not been considered a limiting factor in moist tundra ecosystems (Oberbauer and Dawson 1992).

Under existing environmental conditions, microsite significantly affected photosynthesis in all three sedge species. Net assimilation and g_s tended to be greater in the hollows than on the hummocks, which suggests that these species may be better adapted to the colder, wetter growing conditions found there. Our results agree with the observations of Shaver et al. (1979), who found that Carex aquatilis biomass was greater in colder, rather than warmer, microsites. In the hummock-hollow system at Alexandra Fiord, however, sedge biomass is significantly higher on the hummocks than in the hollows (pers. obs.), suggesting that factors other than direct effects of temperature on photosynthesis are operating. Previous studies indicate that sedge growth is strongly limited by the oligotrophic nature of their environments, and that even small nutrient additions can result in a significant increase in biomass (Henry et al. 1986b, 1990, Chapin and Shaver 1985, Shaver et al. 1986a). We suspect that the long-term, cumulative effect of the substantial differences in soil temperature we measured between hummocks and hollows may be sufficient to improve nutrient availability and stimulate biomass production, but only in the hummocks. Henry and Svoboda (1986b) found significantly greater rates of nitrogen fixation (acetylene reduction) in hummocks than hollows in the same meadow site at Alexandra Fiord.

Experimental warming affected photosynthesis of Carex stans and Eriophorum triste, but the effects differed by species and microsite. Warming significantly depressed photosynthesis in Eriophorum, regardless of microsite. On the other hand, warming tended to increase NA in Carex stans on hummocks, but depressed assimilation for plants growing in the hollows. Chapin and Shaver (1985) found that increasing growing season temperature

also had a significant, negative influence on the growth of Eriophorum angustifolium, but had no effect on Carex aquatilis.

In this study, g_s in sedges appeared to be quite sensitive to fluctuations in temperature, declining as air temperature rose; however, experimental warming had no effect on g_s. Stomatal conductance was only loosely correlated with NA , which suggests that photosynthesis was affected more by non-stomatal limitations than by the direct stomatal function. Johnson and Caldwell (1975) found little decline in assimilation in Carex aquatilis with large increases in vapour pressure deficits, and attributed declining assimilation rates to low soil moisture. In our study, soil moisture was probably not limiting, indicated by no differences in Ψ_L among experimental treatments.

At Alexandra Fiord, enhanced summer air temperatures associated with climate change may have a negative effect on productivity of Eriophorum triste (both hummocks and hollows) and Carex stans (hollows only) by depressing photosynthetic rates. However, our temperature data indicate that warmer air may have a much more pronounced effect on hummock plants than those growing in the hollows; although air temperatures were elevated in the OTCs, soil temperature regimes in the hollows were not altered. The longer-term effects remain unclear. On the one hand, elevated air temperature may depress net assimilation and production, but we do not know how dark respiration will respond. In some arctic species, respiration declines with increasing temperature (Mawson et al. 1986), which could modify the negative effects of temperature on assimilation. If the active layer deepens and soil moisture declines sufficiently, water stress could also have a negative impact.

On the other hand, increases in soil temperature on the hummocks will probably lead to improved soil nutrient status, in part by accelerating decomposition and N-fixation rates (Henry and Svoboda 1986b), which in turn would likely have a positive influence on sedge growth. Elevated atmospheric CO_2 concentrations may have little or no long-term effect on photosynthesis in tundra ecosystems (Billings et al. 1984, Grulke et al. 1990, Oechel et al. 1992). However, new tillering in Eriophroum vaginatum was stimulated by CO_2 and

warming within one growing season, without the addition of nutrients (Tissue and Oechel 1987). Fetcher and Shaver (1990) have suggested that productivity of sites dominated by Eriophorum vaginatum in northern Alaska might be limited under climate warming, at least until other ecotypes able to respond favorably to ameliorated growing conditions, and can replace current populations. Under enhanced atmospheric CO_2, photosynthesis may be stimulated only if additional nutrients are readily available (Oberbauer et al. 1986), or if sink strength in growing tillers or leaves is not inhibited by cold temperatures (Farrar and Williams 1991).

Table 4.1. Results of repeated-measures ANOVA for gas exchange variables measured for control sedges only, on hummocks and in hollows, measured 7-8 July 1992.

		GAS EXCHANGE VARIABLES								
		NET ASSIMILATION			STOMATAL CONDUCTANCE			RESIDUAL CONDUCTANCE		
SPECIES	SOURCE	df	F	P	df	F	P	df	F	P
Carex aquatilis stans	Within-subjects									
	Time	5	17.35	0.0001	5	8.99	0.0007	5	17.7	0.0001
	Time x Position	5	10.4	0.4036	5	0.32	0.7638	5	1.02	0.4161
	Between-subjects									
	Position	1	2.24	0.1655	1	1.41	0.2642	1	2.17	0.1712
Carex membranacea	Within-subjects									
	Time	5	12.46	0.0001	5	18.31	0.0001	5	12.9	0.0001
	Time x Position	5	0.23	0.9676	5	0.79	0.5389	5	0.22	0.9378
	Between-subjects									
	Position	1	5.85	0.0361	1	4.31	0.0646	1	5.84	0.0363
Eriophorum angustifolium triste	Within-subjects									
	Time	5	16.81	0.0001	5	13.12	0.0001	5	170.8	0.0001
	Time x Position	5	1.05	0.3986	5	0.28	0.8658	5	1.04	0.0454
	Between-subjects									
	Position	1	7.99	0.0181	1	1.77	0.2128	1	8.03	0.0172

Table 4.2. Results of ANOVA of gas exchange variables for sedges on hummocks and in hollows, in OTCs and control plots, measured 4-6 July 1993.

		GAS EXCHANGE VARIABLES											
		NET ASSIMILATION			STOMATAL CONDUCTANCE			RESIDUAL CONDUCTANCE			LEAF WATER POTENTIAL		
SPECIES	SOURCE	df	F	P	df	F	P	df	F	P	df	F	P
Carex aquatilis stans	Between-subjects												
	Position	1	3.91	0.0496	1	12.39	0.0005	1	3.94	0.0484	1	0.31	0.5784
	Warming	1	0.79	0.3745	1	2.44	0.1199	1	0.69	0.4088	1	0.11	0.7463
	Pos x Warm	1	6.91	0.0093	1	0.91	0.3403	1	6.78	0.0099	1	0.09	0.7709
	Time	11	3.51	0.0002	11	9.89	0.0001	11	3.61	0.0001	11	1.59	0.1322
	Pos x Time	11	3.04	0.0009	11	0.61	0.8191	11	3.01	0.0011	11	0.91	0.5392
	Warm x Time	11	1.95	0.0354	11	1.73	0.0696	11	1.94	0.0365	11	0.17	0.9985
	Pos x Warm x Tim	11	0.99	0.4586	11	0.54	0.8728	11	0.98	0.4691	11	0.51	0.8842
Eriophorum angustifolium triste	Between-subjects		1.15										
	Position	1	7.13	0.2843	1	3.72	0.0551	1	1.18	0.2781	1	0.11	0.7383
	Warming	1	0.14	0.0082	1	0.01	0.9539	1	7.14	0.0082	1	1.27	0.2649
	Pos x Warm	1	3.75	0.7101	1	0.57	0.4522	1	0.17	0.6812	1	0.91	0.3459
	Time	11	1.77	0.0001	11	17.79	0.0001	11	3.83	0.0001	11	1.51	0.1641
	Pos x Time	11	0.98	0.0615	11	0.93	0.5127	11	1.73	0.0698	11	3.16	0.0028
	Warm x Time	11	1.02	0.4706	11	1.05	0.4006	11	0.97	0.4761	11	1.14	0.3562
	Pos x Warm x Tim	11		0.4299	11	0.61	0.8186	11	1.02	0.4265	11	1.25	0.2821

Figure 4.1. Soil temperature (3 cm) in and out of OTCs during 1992 and 1994. Solid lines are for OTCs; dotted lines are control plots. Data are means (± SE).

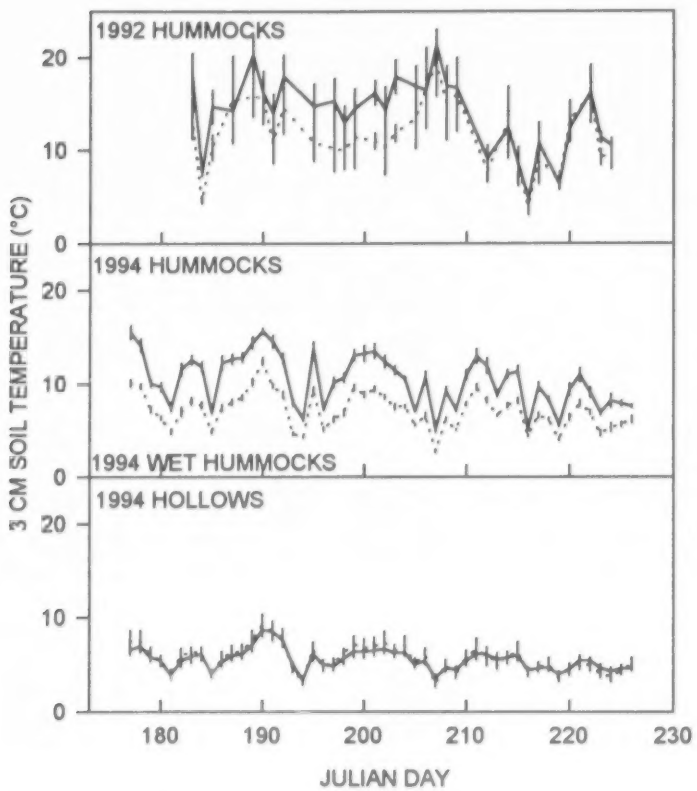


Figure 4.2. Sedge diurnal gas exchange variables (means ± SE) measured 7-8 July 1992 in control plots only. N=12 for each species. Leaf temperatures are means for all three species in both warming treatments; error bars not visible.

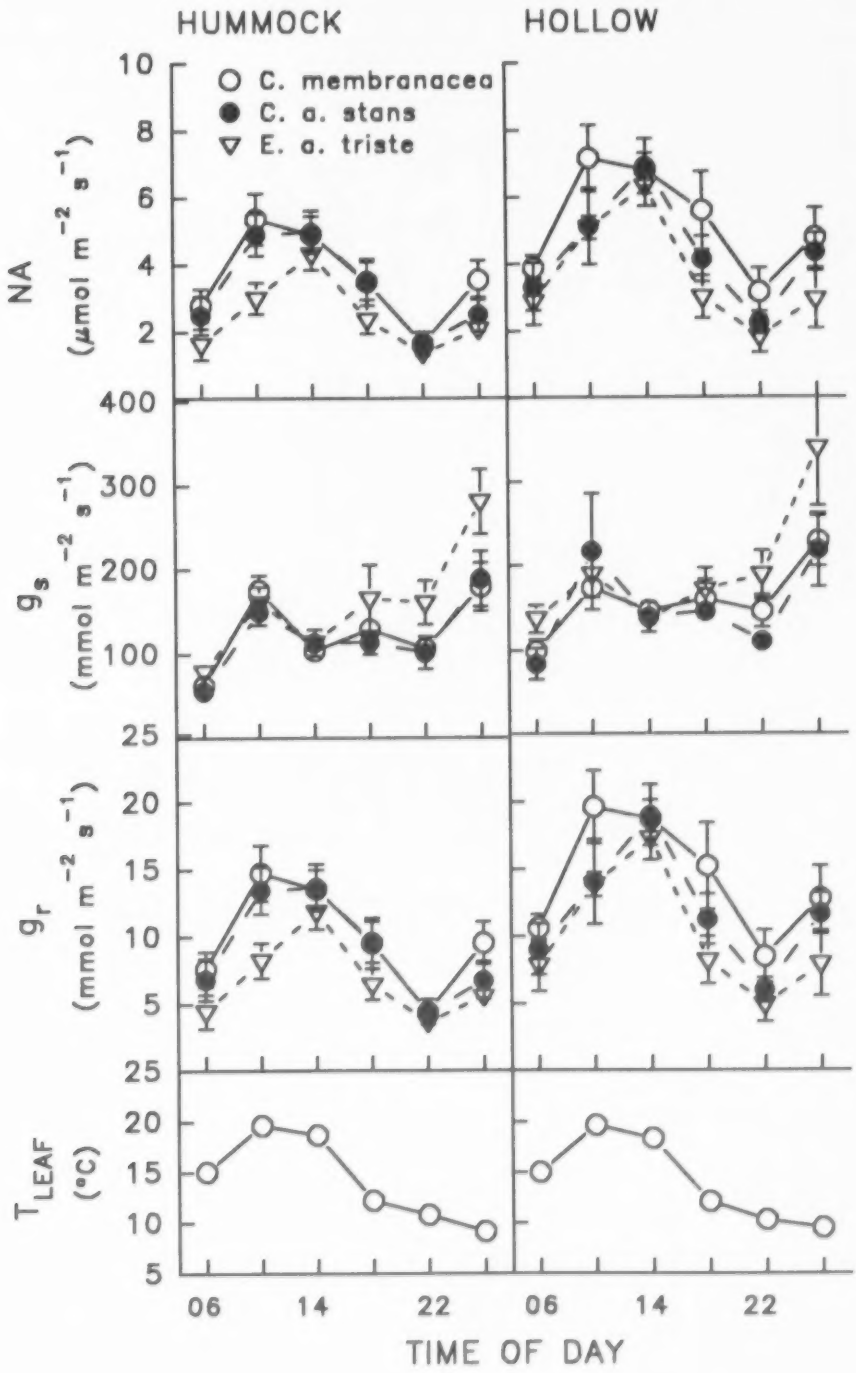


Figure 4.3. Net assimilation (NA) for Carex aquatilis stans and Eriophorum angustifolium triste on hummocks and in hollows, in OTCs and control plots, measured 4-6 July 1993. Data are means (± SE); n=5.

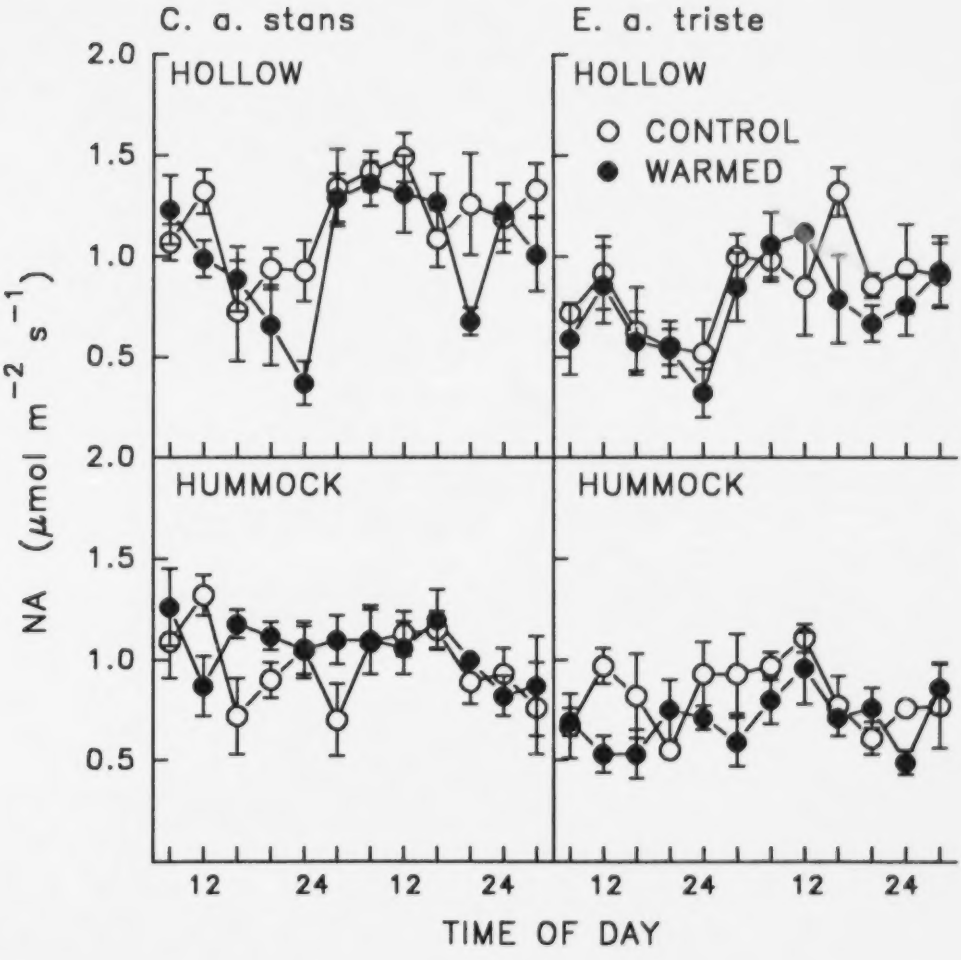


Figure 4.4. Residual conductance (g_r) for Carex aquatilis stans and Eriophorum angustifolium triste on hummocks and in hollows, in OTCs and control plots, measured 4-6 July 1993. Data are means (± SE); n=5.

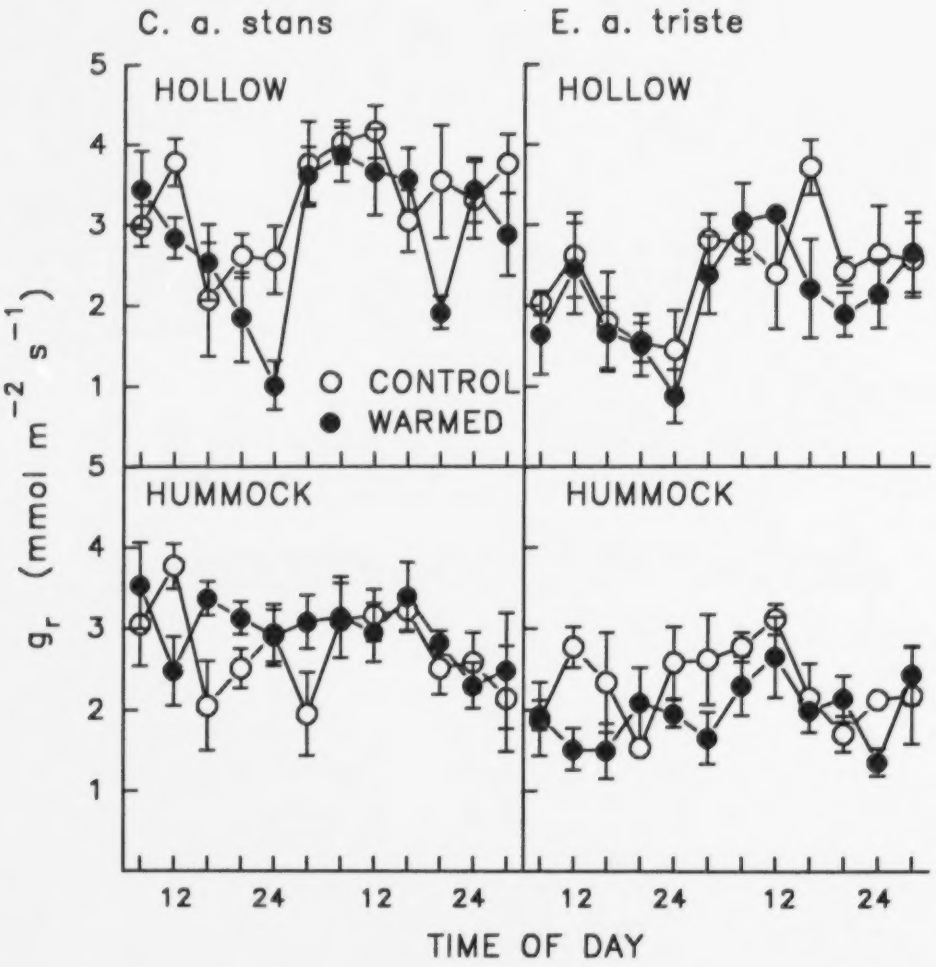


Figure 4.5. Stomatal conductance (g_s) for Carex aquatilis stans and Eriophorum angustifolium triste on hummocks and in hollows, in OTCs and control plots, measured 4-6 July 1993. Data are means (± SE); n=5.

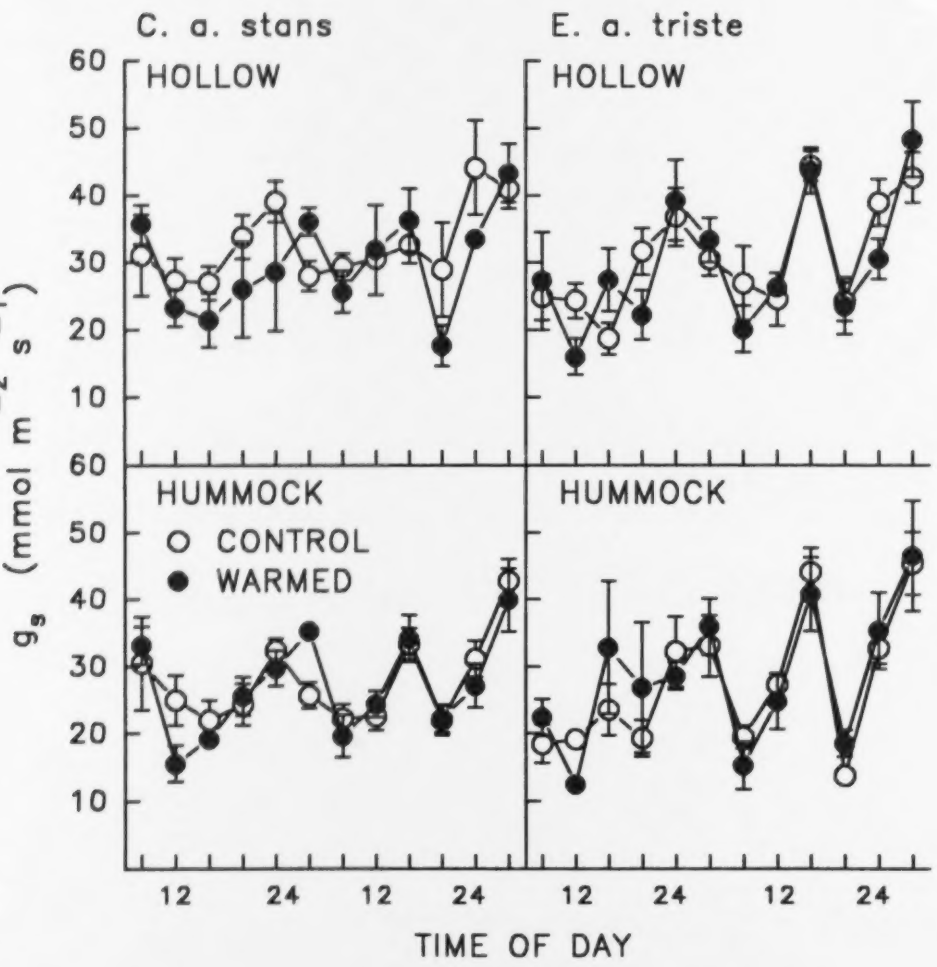
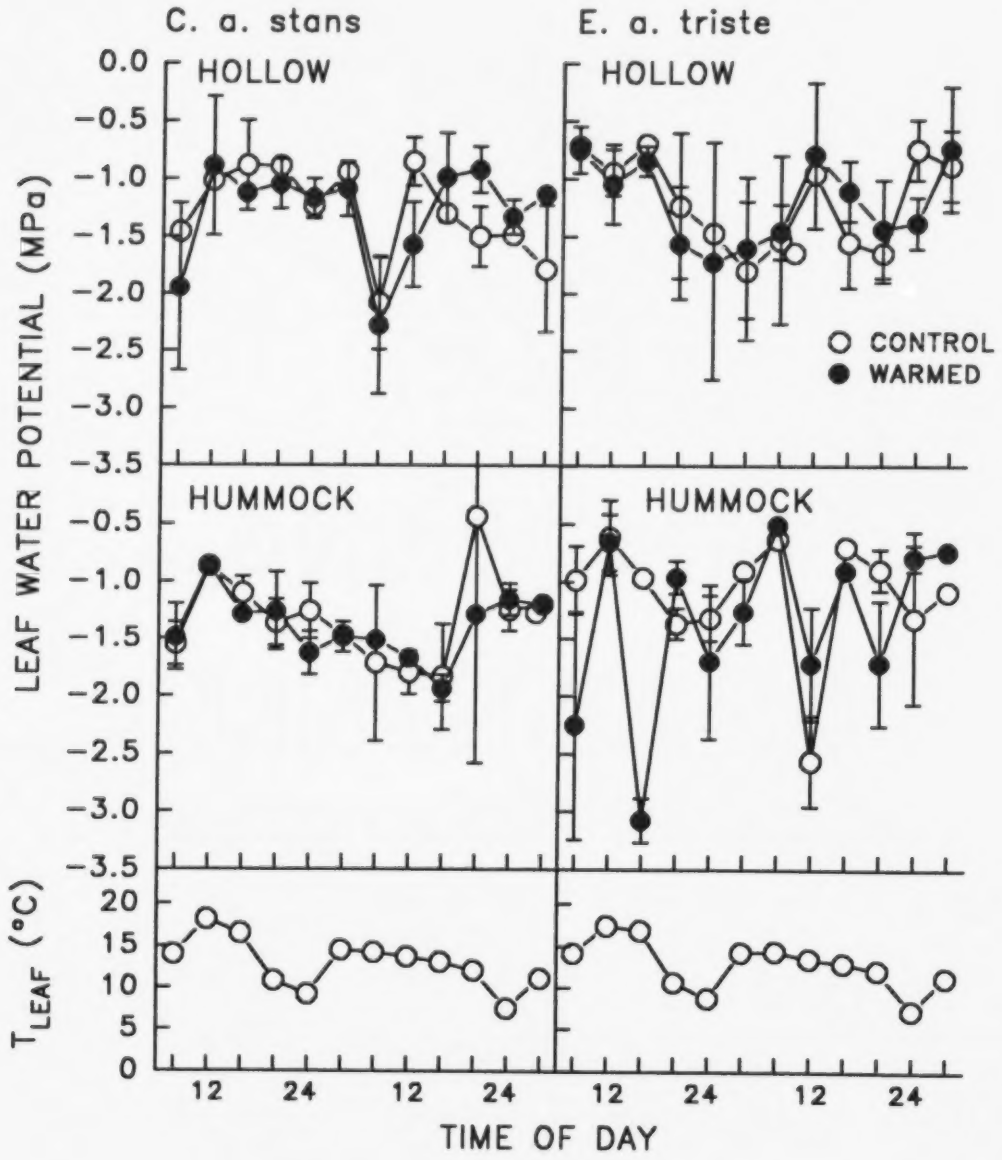


Figure 4.6. Leaf water potentials and leaf temperatures for Carex aquatilis stans and Eriophorum angustifolium triste on hummocks and in hollows, in OTCs and control plots, measured 4-6 July 1993. Data are means (± SE); n=5. Leaf temperatures are means for both species in both experimental treatments; error bars not visible.



References

Beadle, C. L., R. E. Neilson, H. Talbot, and P. G. Jarvis. 1985. Stomatal conductance and photosynthesis in a mature Scots pine forest. I. Diurnal, seasonal and spatial variation in shoots. Journal of Applied Ecology **22**:557-571.

Billings, W. D., K. M. Peterson, J. O. Luken, and D. A. Mortensen. 1984. Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. Oecologia **65**:26-29.

Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology **66**:564-576.

Chapin, F. S., III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver, and J. Svoboda. 1992. Arctic plant physiological ecology in an ecosystem context. Pages 441-451 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Dang, Q. L., V. J. Lieffers, R. L. Rothwell, and S. E. Macdonald. 1991. Diurnal variation and interrelations of ecophysiological parameters in three peatland woody species under different weather and soil moisture conditions. Oecologia **88**:317-324.

Farrar, J. F., and M. L. Williams. 1991. The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. Plant, Cell and Environment **14**:819-830.

Fetcher, N., and G. R. Shaver. 1982. Growth and tillering patterns within tussocks of Eriophorum vaginatum. Holarctic Ecology **5**:180-186.

---. 1990. Environmental sensitivity of ecotypes as a potential influence on primary productivity. The American Naturalist **136**:126-131.

Grulke, N. E., G. H. Riechers, W. C. Oechel, U. Hjelm, and C. Jaeger. 1990. Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. Oecologia **83**:485-494.

Henry, G. H. R. 1987. Ecology of sedge meadow communities of a polar desert oasis: Alexandra Fiord, Ellesmere Island, Canada. Ph.D. Dissertation. University of Toronto, Toronto, Canada.

---. 1994. Comparisons of grazed and non-grazed high-arctic sedge meadows. Pages 193-194 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, ONT.

Henry, G., B. Freedman, and J. Svoboda. 1986a. Survey of vegetated areas and muskox populations in east-central Ellesmere Island. Arctic **39**:78-81.

Henry, G. H. R., and J. Svoboda. 1986b. Dinitrogen fixation (acetylene reduction) in high arctic sedge meadow communities. Arctic and Alpine Research **18**:181-187.

Henry, G. H., J. Svoboda, and B. Freedman. 1990. Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. Canadian Journal of Botany **68**:2660-2667.

Johnson, D. A., and M. M. Caldwell. 1975. Gas exchange of four arctic and alpine tundra plant species in relation to atmospheric and soil moisture stress. Oecologia **21**:93-108.

Jones, H. G. 1985. Partitioning stomatal and non-stomatal limitations to photosynthesis. Plant, Cell and Environment **8**:95-104.

Labine, C. 1994. Meteorology and climatology of the Alexandra Fiord lowland. Pages 23-40 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, ONT.

Marion, G. M., G. H. R. Henry, P. Molgaard, W. C. Oechel, M. H. Jones, and G. L. Vourlitis. 1993. Open-top devices for manipulating field temperatures in tundra ecosystems. Lunardini,V.J. and S.L. Bowen, eds. Proceedings, Fourth International Symposium on Thermal Engineering and Science for Cold Regions, 28 Sept.-1 Oct. 1993. U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH. (205-210)

Mawson, B. T., J. Svoboda, and R. W. Cummins. 1986. Thermal acclimation of photosynthesis by the arctic plant Saxifraga cernua. Canadian Journal of Botany **64**:71-76.

Maxwell, B. 1992. Arctic climate: potential for change under global warming. Pages 11-34 *in* F. S. I. I. I. Chapin, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, CA.

Mayo, J. M., A. P. Hartgerink, D. G. Despain, R. G. Thompson, E. M. Z. Bakker, and S. D. Nelson. 1977. Gas exchange studies of Carex and Dryas, Truelove Lowland. Pages 265-280 *in* L. C. Bliss, editor. Truelove Lowland, Devon Island, Canada: a High Arctic ecosystem. University of Alberta Press, Edmonton.

McGraw, J. B., and N. Fetcher. 1992. Response of tundra plant populations to climatic change. Pages 359-376 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Muc, M., J. Svoboda, and B. Freedman. 1994a. Aboveground standing crop in plant communities of a polar desert oasis, Alexandra Fiord, Ellesmere Island. Pages 65-74 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, ONT.

---. 1994b. Soils of an extensively vegetated polar desert oasis, Alexandra Fiord, Ellesmere Island. Pages 41-50 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis. Captus University Publications, Toronto.

Oberbauer, S. F., and T. E. Dawson. 1992. Water relations of arctic vascular plants. *in* Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Oberbauer, S., and P. C. Miller. 1979. Plant water relations in montane and tussock tundra vegetation types in Alaska. Arctic and Alpine Research **11**:69-81.

Parsons, A. N., J. M. Welker, P. A. Wookey, M. C. Press, T. V. Callaghan, and J. A. Lee. 1994. Growth responses of four sub-arctic dwarf shrubs to simulated environmental change. Journal of Ecology **82**:307-318.

Shaver, G. R., F. S. Chapin III, and W. D. Billings. 1979. Ecotypic differentiation in Carex aquatilis on ice-wedge polygons in the Alaskan coastal tundra. Journal of Ecology **67**:1025-1045.

Shaver, G. R., F. S. Chapin III, and B. L. Gartner. 1986a. Factors limiting seasonal growth and peak biomass accumulation in Eriophorum vaginatum in Alaskan tussock tundra. Journal of Ecology **74**:257-278.

Shaver, G. R., N. Fetcher, and F. S. Chapin III. 1986b. Growth and flowering in Eriophorum vaginatum: annual and latitudinal variation. Ecology **67**:1524-1535.

Svoboda, J., and B. Freedman, editors. 1994. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus University Publications, Toronto.

Tieszen, L. L. 1975. CO2 exchange in the Alaskan arctic tundra: seasonal changes in the rate of photosynthesis of four species. Photosynthetica **9**:376-390.

von Caemmerer, S., and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta **153**:376-387.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113-137 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York.

Walker, M. D., P. J. Webber, E. H. Arnold, and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology **75**:393-408.

Wielgolaski, F. E., L. C. Bliss, J. Svoboda, and G. Doyle. 1981. Primary production of tundra. Pages 187-225 *in* L. C. Bliss, O. W. Heal and J. J. Moore, editors. Tundra ecosystems: a comparative analysis. Cambridge University Press, London.

CHAPTER 5

Gas exchange responses of a high arctic willow, Salix arctica, to elevated atmospheric CO_2 and temperature in controlled environments

Introduction

Although a great deal is currently understood about temperate plant responses to elevated atmospheric CO_2 concentrations, very few studies have examined the responses of arctic vegetation. This is in spite of the fact that a doubling of global atmospheric CO_2 is likely to have more pronounced effects in the arctic than in any other region. General circulation models indicate that elevated CO_2 will lead to an increase in summer temperatures of up to 5°C, and increases in winter temperatures in the range of 6-14°C in the High Arctic (Maxwell 1992). How might arctic vegetation, adapted to short, cold growing seasons, respond to these changes? The adaptations that allow arctic species to survive in their extreme environments may influence their ability to adjust to an altered climate. For example, photosynthesis in arctic species is generally less sensitive to environmental temperature variation than temperate species (Semikhatova et al. 1992). Plant biomass often increases in response to enhanced air temperatures, but other environmental factors usually constrain the magnitude and duration of the response (Oechel and Billings 1992). Driven by elevated temperature and increased precipitation that should accompany climatic changes, alterations in growing season length, soil temperature, active layer depth, soil moisture and nutrient availability have the potential for substantially altering arctic environments (Chapin et al. 1992b). These indirect effects of global climate change may ultimately have more of an impact on arctic vegetation than the direct effects of enhanced CO_2 and temperature on photosynthesis and growth (Shaver and Kummerow 1992).

Direct experimental manipulation of tundra vegetation with elevated atmospheric CO_2 concentrations has been remarkably limited. Several studies have examined small-scale ecosystem responses to elevated CO_2 (Billings et al. 1982, 1983, Hilbert et al. 1987, Grulke et al. 1990, Oechel et al. 1992). In

these studies, carbon assimilation declined to levels found in plants grown at ambient CO_2 after a period of three weeks to three years.

In one of two species-level studies, Tissue and Oechel (1987) manipulated CO_2 and temperature for Eriophorum vaginatum under field conditions in Alaskan tussock tundra. This study also found a downward adjustment of photosynthesis, in this case after three weeks, although tillering increased significantly in the CO_2 treatments. The other study of arctic vegetation response to elevated CO_2 was conducted in controlled environments, without temperature as an experimental factor. Oberbauer et al. (1986) found that although growth was stimulated by nutrient additions, enhanced CO_2 had no additional effect; photosynthesis rates depended on CO_2 level and nutrient treatment.

Variability among the species examined by Oberbauer et al. (1986) support the conclusions of Chapin and Shaver (1985), who found that arctic species respond individualistically to environmental manipulations including temperature and nutrients. Examining CO_2 and temperature together is important in climate change studies of photosynthesis since any increases in air temperature will be driven by increases in atmospheric CO_2 concentrations (Long 1991). Further study is clearly required to determine if other arctic species or growth forms respond similarly to those examined in the above studies, and whether habitats other than tussock tundra have an influence on plant performance.

In this controlled environment study we examined the gas exchange responses of Salix arctica, a dwarf willow important in many plant communities in the High Arctic, to atmospheric CO_2 concentrations and air temperatures reflecting existing and predicted future climates. Our objective was to determine whether enhanced CO_2 and temperature had an effect on photosynthesis, stomatal conductance, and dark respiration, and whether the strength of the response differed by original habitat from which the plants were taken. Ours is the first study to examine photosynthesis of any high arctic species in response to elevated CO_2.

In field studies with Salix arctica, we found that enhanced growing season temperature had positive or negative influences on gas exchange, depending on the habitat and sex of the plants (Chapter 3). Generally, photosynthesis and stomatal conductance were affected by warming more strongly in the wet habitat than in the dry. Evidence from previous studies indicate that S. arctica and other tundra species may also be sensitive to changes in soil moisture and temperature, depending on their habitat (Oberbauer and Dawson 1992). Furthermore, ecotypic differentiation can have a substantial impact on plant performance under current environmental conditions (McGraw and Fetcher 1992).

We examined the responses of a cohort of leaves over a range of leaf ages in order to (i) determine whether, as indicated by other studies with enhanced atmospheric CO_2, a downward shift in photosynthesis occurs within a single growing season, and (ii) to assess the relative potential contribution of leaf age to plant productivity. Leaf age has previously been shown to have a significant influence on gas exchange and water relations properties in Salix arctica under ambient CO_2 (Dawson and Bliss 1993), an effect also found in other species (Field 1987, Farrar and Williams 1991, Kelly et al. 1991). In the first part of this study we examined plants under well-watered conditions in order to eliminate potential confounding effects of water limitations on photosynthesis and stomatal conductance (Ögren and Öquist 1985, Guehl et al. 1994). We subsequently withheld water in order to examine the response of this species to soil drying. Plant water relations are likely to play a significant role in ecosystem function under a changed climate, particularly in polar desert, semidesert, or other xeric communities (Oberbauer and Dawson 1992). Salix arctica has tissue elasticity and osmotic adjustment properties which help it to tolerate dry soil and air conditions (Dawson and Bliss 1989).

Based on our own work and that of previous studies, we anticipated that elevated CO_2 would lead to increased net assimilation, and that the strength of this increase should be enhanced by elevated temperature. We further

anticipated that short-term soil drying would not have a significant impact on photosynthesis.

Methods

Study species

The prostrate, dioecious shrub Salix arctica is common in circumpolar regions and, in North America, is the only willow species present north of 80° latitude (Porsild and Cody 1980). Salix arctica was collected at Alexandra Fiord, Ellesmere Island (78°53'N, 75°55'W) in the Canadian Arctic Archipelago. The lowland at Alexandra Fiord is a polar oasis, with generally warmer temperatures and more soil moisture than polar desert or semi-desert, resulting in generally greater plant cover and productivity (Bliss and Matveyeva 1992). An extensive description of the ecology of the Alexandra Fiord lowland can be found in Svoboda and Freedman (1994). We examined plants from two habitats. One is relatively xeric, characterized by minimal snow deposition, early snowmelt, deep early-season active layer, and dry sandy and peaty soils (Muc et al. 1994). Salix arctica is the dominant species in this community. The second habitat is a wet sedge meadow with relatively later snowmelt, cold soils with a later-developing active layer, and typically with surface water flowing most of the growing season. Willows are an important component in this habitat but are restricted to hummocks (Henry et al. 1990).

In late August 1993, relatively small, senescing willows were excavated and trimmed of roots and branches longer than 15 cm. Care was taken to retain stems with viable buds and as many small roots as possible. Specimens were sealed in plastic bags with moistened paper towels and kept in chilled coolers until being returned to the lab three days later. Plants were then stored in the dark at -2°C for 12 weeks before being moved to 5°C for 36 h prior to potting. Specimens were planted in 6" (155mm) standard plastic pots in a 7:1 mixture of Terra-Lite Metro Mix 220 (Grace Horticultural Products, Ajax, Ontario, Canada) and pasteurized topsoil. Cut root ends larger than

approximately 3 mm were treated with 0.4% indole butyric acid (IBA) to enhance rooting.

Experimental design

Plants were grown in one of four combinations of CO_2 partial pressure and air temperature in controlled environment chambers at the University of Alberta. Eight male and eight female plants from each of the two habitats were randomly selected for inclusion in each experimental treatment (n=32/treatment; N=128), and were placed in the controlled environments immediately after potting. The CO_2 treatment levels reflect existing and predicted atmospheric CO_2 levels, i.e., high CO_2 (HC, 675-725 $\mu l\ L^{-1}\ CO_2$) or low CO_2 (LC, 375-400 $\mu l\ L^{-1}\ CO_2$). Temperature treatments reflected current early-season mean soil temperatures (3 cm) and those found during mid-season; i.e., high temperature (HT, 12°C) or low temperature (LT, 5°C). These temperature differences are slightly greater than predicted since plants in controlled environments do not benefit from warming effects of direct insolation, and increases in air temperature are not reflected by equivalent increases in leaf temperature (Bowes 1991). The resulting four treatment combinations, then, were high temperature + high CO_2 (HTHC), high temperature + low CO_2 (HTLC), low temperature + high CO_2 (LTHC), and low temperature + low CO_2 (LTLC). Temperature, CO_2, and light were held constant throughout each 24 h period; light was provided by high intensity sodium and mercury fixtures in all but the LTLC treatment, which used fluorescent and incandescent lamps. Light levels were approximately 250 $\mu mol\ m^{-2}\ s^{-1}$ at bench height in all chambers, and pots were re-randomized within chambers 10 times during the experiment. Relative humidity was maintained at approximately 75% in each chamber. Soil temperatures in pots were found to be equivalent to air temperatures.

The experiment was conducted in two parts. First, plants were grown under well-watered conditions. Gas exchange was measured on a single cohort of leaves on three occasions, with leaf age and position in fascicle standardized as much as possible across all plants and experimental treatments, since

responses can vary with leaf age (Field 1987, Dawson and Bliss 1993). Measurements were made on the third leaf in a fascicle once it reached full extension, approximately 21 d after bud break (28 d after placement in the growth chambers) and again at 28 and 35 d. Leaves in the high temperature treatments reached full expansion approximately 2 d earlier than those in the low temperature treatments. Plants grown at elevated temperature were measured on the day prior to those in the low temperature treatments. Consequently, reported leaf ages are approximate.

A dry-down experiment was subsequently conducted on a subset of plants from the high temperature treatments (HTHC and HTLC), which produced a second flush of leaves. These plants were watered to field capacity 3 d prior to the start of gas exchange measurements, and then left to dry over time. As with the initial experiment, measurements were conducted on a cohort of leaves of standard age. At the time of the first gas exchange measurement of the dry-down experiment, leaf age was approximately 21 d, although plants had been growing in their respective experimental treatments for approximately 6 wk. Leaf water potential measurements, because they were destructive, were conducted on a separate set of leaves as close to the reported leaf age as possible. Plants were not fertilized during either experiment.

Gas exchange measurements

Net assimilation (NA), stomatal conductance (g_S), and dark respiration (R_D) were measured on attached, intact leaves using a portable, open-system infrared gas analyser (LCA-3, Analytical Development Corporation, Hoddeson, England) and a PLC(C) leaf chamber. Flow rate was maintained at 150 ml sec^{-1} and incoming relative humidity at approximately 20%. Light was maintained at saturating levels (>1350 μmol m^{-2} sec^{-1}) using a 12 volt quartz halogen light (MR-16, Phillips, Sommerset, NJ, USA) affixed to the leaf chamber. Prior to dark respiration measurements, plants were allowed to equilibrate in the dark but within their respective controlled environments for approximately 10 min. During R_D measurements, the leaf chamber was placed in an opaque fabric bag. Calculations for all variables follow von Caemmerer and Farquhar (1981)

and Jones (1985), and are expressed on a projected leaf area basis, using a LI-COR Model 3100 leaf area meter (Lincoln, NE, USA). Leaves were harvested for leaf area measurements on day 35 for the well-watered plants, and on day 19 for those in the dry-down experiment. Leaf water potentials were measured during the dry-down experiment only on a set of leaves separate from those measured for photosynthesis. Small disks cut from leaves were allowed to equilibrate for a minimum of 20 min before being measured psychometrically (HR33T Dew Point Microvoltmeter and C-52 Sample Chambers, Wescor, Logan, Utah, USA).

Gas exchange measurements were conducted at the respective CO_2 treatment levels. During the initial experiment, measurements on plants grown at high CO_2 were conducted inside their controlled environments. Changes in CO_2 concentration inside chambers were prevented by the experimenter wearing a CO_2-absorbing breathing apparatus (Jones et al. 1993). During the dry-down experiment, measurements were conducted outside the controlled environment chambers by passing bottled air of known CO_2 concentration through the leaf chamber. All measurements made at ambient CO_2 concentrations were conducted outside the controlled environments. Since leaf temperatures could not be maintained at experimental treatment levels during gas exchange measurements, they were standardized across all treatments at approximately 22-25°C.

Instantaneous water use efficiency (WUE), the ratio of internal to external CO_2 concentration (C_i/C_a), and specific leaf area (SLA; $m^2\ g^{-1}$) were also calculated. The ratio C_i/C_a was used as a means of examining effects of temperature, CO_2 and a decline in soil moisture on photosynthesis and stomatal acclimation (Sage 1994).

Data analysis

Repeated-measures analysis of variance were conducted on gas exchange variables for both experiments, following von Ende (1993). Within-subjects effects (with time as the repeated factor) were treated in a univariate manner using the Huyhn-Feldt correction for sphericity. Contrasts conducted

for the initial experiment were examined using procedure GLM and an adjusted critical alpha of 0.01274 to restrict the experimentwise error rate to α=0.05 (Sokal and Rohlf 1981). A non-repeated-measures analysis of variance was conducted to test for differences among specific leaf areas, since this variable was measured one time only at the end of each experiment. In both experiments, leaves which were damaged or otherwise unsuitable were no longer included in the experiment. Consequently, the final sample size used in the analyses included only those leaves which were measured on all occasions.

Results

Well-watered conditions

Net assimilation and stomatal conductance were significantly affected by both CO_2 and temperature (Table 5.1). Both variables were consistently higher in the HTHC treatment than in any other treatment across all leaf ages (Fig. 5.1), and neither tended to decline with leaf age. The effect of original field habitat on NA was nearly significant at P=0.0681, due primarily to differences in NA for the HTHC treatment only. In this experimental treatment, plants from the dry habitat had approximately double the NA of their wet habitat counterparts across all three leaf ages (data not shown). However, habitat had no effect on g_S. The levels of NA and g_s observed in this study are only slightly lower than those measured in the field (Chapter 3).

Elevated CO_2 resulted in significantly higher dark respiration, but only at high temperature (Table 5.1). As with NA and g_S, R_D was consistently higher for the HTHC treatment across all leaf ages, and exhibited no decline with time (Fig. 5.1). This was the only variable for which CO_2 and temperature exhibited a significant interaction (Table 5.1). There was substantial variability in R_D among experimental treatments for the youngest leaves, but this was reduced as leaves aged.

Water use efficiency was influenced significantly by CO_2, but not by temperature, and there was no overall effect of leaf age on WUE (Table 5.1). Generally, enhanced CO_2 resulted in better WUE, with the exception of the

youngest leaves at low temperature (Fig. 5.1). The effect of CO_2 was greatest at high temperature (HTHC vs HTLC), and the effect of temperature at high CO_2 (HTHC vs LTHC) was also significant for leaves at 28 d (Table 5.1).

The C_i/C_a ratios were significantly affected by temperature but not CO_2 (Table 5.1). For leaves at 28 d, increased temperature at a given CO_2 concentration resulted in higher C_i/C_a. At 35 d, however, plants grown at elevated CO_2 had slightly lower C_i/C_a than plants at ambient CO_2. Plants from the dry habitat had significantly higher C_i/C_a ratios than those from the wet habitat, regardless of experimental treatment or leaf age. Specific leaf areas (SLA) were significantly affected by CO_2 and temperature (Table 5.1). Leaves grown at lower temperatures had higher SLA than warmer plants, regardless of CO_2 treatment (Fig. 5.2).

Soil drying

Net assimilation was significantly higher for plants grown in the high CO_2 environment (Table 5.2) over the duration of the dry-down experiment (Fig. 5.3). As the soil dried, NA in high CO_2 plants nearly doubled for a period of 5 days, before declining by day 13 to the same level measured under well-watered conditions. In contrast, NA for the low CO_2 plants remained fairly constant. Stomatal conductances declined significantly over the course of this experiment, but the effect of CO_2 was not significant. Water use efficiency did not differ significantly between experimental treatments and did not change significantly with time. The effects of CO_2 and time were not significant for Ψ_L. However, leaf water potentials increased slightly during the first week of drying, as g_s remained steady or declined, and only after 19 d did Ψ_L return to levels found in well-watered plants. We observed no effect of CO_2 on C_i/C_a, although C_i/C_a did decline significantly, however slightly, over the course of the experiment. The effect of CO_2 on SLA was not significant.

Discussion

Net assimilation was significantly higher in Salix arctica grown in the high temperature + high CO_2 treatment, and appears to be influenced strongly by both variables. Elevated temperature alone had no effect on NA in Salix arctica in this study. However, in our field experiments with this species, experimental warming had significantly positive effects on NA for female willows in the dry habitat, and significantly negative effects in the wet habitat; male willows were less affected by temperature (Chapter 3).

Our results are in contrast to responses of other arctic species. Eriophorum vaginatum showed essentially no effect of enhanced CO_2 and temperature on assimilation (Tissue and Oechel 1987). Photosynthesis was depressed or unchanged in Ledum palustre, Betula nana, and Carex bigelowii when grown at elevated CO_2 under relatively high temperatures and low levels of added nutrients; at high nutrient levels, photosynthesis increased in all but Betula (Oberbauer et al. 1986). In most other species, assimilation typically increases in response to CO_2 enrichment, as long as other environmental factors (e.g., nutrients, water) are not limiting (Strain and Thomas 1992). In this regard, Salix arctica responds more similarly to temperate woody species than other arctic species examined so far (Drake 1992). Although we did not test for it, the high NA observed at elevated CO_2 and 12°C could reflect a shift in the temperature optimum for photosynthesis attributable to CO_2 enrichment (Long 1991, Idso and Idso 1994).

It is not known why NA was not stimulated by CO_2 enrichment at 5°C. Source activity, phloem transport, and sink strength are strongly affected by temperature (Farrar and Williams 1991), and the low temperature treatments in this study may have been sufficient to restrict these processes and cause end-product inhibition of photosynthesis (Bowes 1991; but see Stitt 1991). Because we began the experiment with plant material without intact root systems, we assumed that new root growth would provide a substantial sink for photosynthate. In fact, we observed (but did not quantify) substantially greater root growth for plants growing in the high temperature treatments, with

relatively greater root growth at elevated CO_2. This was not surprising since root:shoot ratios typically increase with CO_2 enrichment (Oberbauer et al. 1986, Tissue and Oechel 1987). Pot size did not appear to restrict photosynthesis (Arp 1991, Sage 1994), since high NA was sustained at elevated temperature and CO_2. The greater specific leaf areas we found at low temperature may reflect an accumulation of photosynthate due to limited sink strength (Farrar and Williams 1991).

No downward regulation of NA occurred over time for the Salix arctica plants grown at elevated CO_2, unlike the responses of other arctic and temperate plants (Tissue and Oechel 1985, Grulke at al. 1990, Oechel et al 1992, Woodward et al. 1991). In fact, we observed little change in NA within experimental treatments across all leaf ages, with the exception of a marked decline in NA in the low temperature + low CO_2 treatment. Because we do not know the photosynthetic responses of these plants prior to 21 d, before leaves reached full expansion, we cannot say with certainty that the NA values we measured were at their maximum. However, the ages of leaves in this study coincide with the ages at which maximum NA occurred in Salix arctica grown in controlled environments at ambient CO_2 (Dawson and Bliss 1993). Continuous, high assimilation rates throughout a growing season could be adaptive for arctic plants, and this is in fact the case for many species (Semikhatova et al. 1992). However, delayed senescence induced by elevated CO_2 could have negative consequences if plants fail to retranslocate foliar nutrients and harden off before autumn frosts (Grulke et al. 1990).

Why NA declined in the low temperature + low CO_2 plants is uncertain. Relatively high levels of NA in the youngest leaves might have been supported by normal early-season root nutrient reserves remaining from their previous summer growing season (Kielland and Chapin 1992). Once depleted, poor root development in the colder soil may have restricted nutrient uptake sufficiently to limit adequate assimilation. Similarly, inadequate root development in the cold soil probably contributed to high variability in WUE and R_D at 21 d in the low temperature + low CO_2 plants. On the other hand, the plants in the low

temperature + low CO_2 treatment may reasonably represent the ability of S. arctica to grow under cold conditions; plants in the elevated temperature and CO_2 treatments may have had delayed senescence, results which are consistent with some field studies (Grulke et al. 1990, Woodley and Svoboda 1994).

Dark respiration rates were high only in the high temperature + high CO_2 treatment, and may reflect the increase in energy required for active loading of phloem for transport of photosynthate out of leaves caused by elevated NA in this treatment (Farrar and Williams 1991, Woodward et al. 1991). Most reports in the literature indicate that R_D declines during both short and long term exposure to elevated CO_2 (Drake 1992). However, several arctic species are reported to have higher R_D at elevated CO_2, relative to ambient, at 15°C (Oechel and Strain 1985). Increased temperature alone also resulted in higher respiration rates for several arctic species, including S. arctica (Dawson and Bliss 1993, Limbach et al. 1982, McNulty and Cummins 1987, but see McNulty et al. 1988).

In surprising contrast to a reduction in g_s typical for plants grown in elevated CO_2 (Morrison 1987), stomatal conductance to water vapor in well watered Salix arctica was stimulated significantly by CO_2 enrichment, but the strength of the effect was dependent upon temperature. Few studies report increased g_s in response to elevated CO_2 (Eamus and Jarvis 1989), and Norby and O'Neill (1991) suggest that elevated g_s may be influenced more by the effects of CO_2 on whole plant water relations, influenced by root:shoot ratios, than by direct effects on g_s. Our results are consistent in this respect since we found (qualitatively) higher g_s in willows with greater root growth. Under ambient CO_2, our results agree with the observation that low root temperature depresses g_s in Salix arctica under field conditions (Dawson and Bliss 1989a). Confounding this, however, are the effects of experimental warming under field conditions at Alexandra Fiord, where the g_s in willows in the wet habitat was negatively affected by increased temperature (Chapter 3).

Stomatal conductance is also sensitive to, and in turn affects, the intercellular CO_2 concentration C_i (Morrison 1987, Sage 1994). Although significantly different, the C_i/C_a ratios in this study differed less than 1% among experimental treatments across all leaf ages, indicating that under well-watered conditions, stomates were sensitive to the increased demand for carbon stimulated by elevated CO_2, and that photosynthesis consumed the additional CO_2.

When water was withheld, stomatal conductance did not differ between CO_2 treatments. Stomatal conductance declined gradually from the outset of the dry-down experiment, and probably helped to maintain Ψ_L above initial levels until the end of the experiment (Dawson and Bliss 1989). The absence of a marked decline in C_i/C_a ratios and the lack of a significant difference between CO_2 treatments suggests that stomatal closure probably had little impact on NA in this experiment. The absolute values of C_i/C_a in this study were high compared to other studies (Norby and O'Neill 1991, Sage 1994). Relative to temperate species, high C_i/C_a ratios might indicate an adaptation on the part of Salix arctica to make as much carbon available for photosynthesis as possible. This view is consistent with the idea that arctic plants are well-adapted to rapid completion of growth in their short, cold, but highly variable growing seasons (Semikhatova et al. 1992).

The cause of the initial increase in net assimilation in plants grown at high CO_2 (+12°C) when water was withheld is unclear. Although these plants did not appear to be water stressed, the consensus from the literature indicates that growth is stimulated more by elevated CO_2 when water is slightly limiting than when it is not (Idso and Idso 1994). Why NA eventually declined is also unclear, but may be due a rate-limiting reduction in soil moisture facilitated by the larger root mass in the high CO_2 plants. Even though a depletion of soil moisture (not measured in this study) was not reflected in $\Psi_{L,}$, NA may nevertheless have been affected (Chaves 1991). Alternatively, P and N availability for rubisco or RuBP may have been reduced sufficiently to directly

affect NA (Oberbauer et al. 1986, Bowes 1991), caused by larger root biomass and incorporation of these elements into plant tissue. If this is the case, our results would be consistent with other studies which have suggested that nutrients may limit, but not eliminate, effects of elevated CO_2 (Kirschbaum 1994).

Some effects of the original habitat from which the willows were taken are apparent in the well-watered plants only. The overall effect of habitat on NA was significant at $P<0.07$ (Table 5.1), and mean values for NA in the high temperature + high CO_2 treatment are nearly double for plants from the dry habitat when compared to those from the wet meadow. There were no habitat differences for NA within the other experimental treatments, however. Nevertheless, this observation suggests that willows from the dry habitat could be more responsive to increased CO_2 and temperature than plants from the wet meadow under climate change. In field studies with Salix arctica under ambient CO_2, we found significant effects of experimental warming on NA for willows growing in both habitats, but the results differed by sex (Chapter 3).

It is difficult to extend observations made in controlled environments to plants growing under field conditions. Indeed, a number of recent papers have reviewed the response differences between field and growth chamber studies (e.g., Strain and Thomas 1992, Drake 1992, Curtis, in prep.). Nevertheless, our results suggest that a doubling of atmospheric CO_2 accompanied by an increase of 4°C in summer air temperature in the arctic would probably be sufficient to significantly stimulate net assimilation in arctic willow under field conditions, at least initially. We do not know whether Salix arctica would respond differently under gradual increases in these variables, or whether an increase in NA would result in enhanced growth, survival, or competitive advantage.

Several factors could constrain the ability of Salix arctica, and other arctic species, to respond favorably to climate change, particularly since predictions are more certain of increases in atmospheric CO_2 concentrations than increases in air and soil temperatures. Enhanced rooting temperatures

will be important for increasing soil nutrients necessary to support additional biomass stimulated by CO_2 enrichment (Chapin and Bledsoe 1992, Kielland and Chapin 1992, Nadelhoffer et al. 1992). The magnitude and duration of plant growth and reproductive responses will undoubtedly depend on increased nutrient availability (Henry et al. 1986, Oberbauer et al. 1986, Chapin et al. 1992, Silvola and Ahlholm 1992, Wookey et al. 1993). If temperatures do not rise sufficiently, or are limited by a shorter growing season caused by increased snowfall, potential increases in biomass would likely be prevented. A negative feedback could also occur should aboveground biomass increase sufficiently to shade and, through increased litter accumulation, insulate the surface (Chapin et al. 1992).

Table 5.1. Results of ANOVA of gas exchange variables for Salix arctica under well-watered conditions in controlled environments. For clarity, only P<0.10 shown. *Because SLA was measured only after 35 d, there are no P values for within-subjects effects.

		NA	gs	WUE	Rd	Ci/Ca	SLA*
BETWEEN SUBJECTS EFFECTS	DF	P	P	P	P	P	P
HABITAT	1	0.0681				0.0121	
TEMP	1	0.0028	0.0001			0.0001	0.0001
H X T	1						
CO2	1	0.0012	0.0059	0.0464	0.0001		0.0042
H X CO2	1						
TEMP X CO2	1				0.0067		
H X T X CO2	1						
ERROR	72						
WITHIN-SUBJECTS EFFECTS							
TIME	2				0.0001	0.0016	
TIME X HABITAT	2	0.0931		0.0283			
TIME X TEMP	2	0.0145	0.0116	0.0219	0.0377	0.0001	
TIME X H X T	2						
TIME X CO2	2		0.0166	0.0212		0.0001	
TIME X H X CO2	2						
TIME X TEMP X CO2	2		0.0001	0.0302			
TIME X H X T X CO2	2						
ERROR	144						
EFFECTS OF	TIME						
CO2 AT HIGH TEMP	1	1			0.0001		
	2	1					
	3	1	0.0001	0.0022	0.0064		0.0175
CO2 AT LOW TEMP	1	1			0.0001	0.0001	
	2	1		0.0009			
	3	1	0.0001	0.0001		0.0049	0.0001
TEMP AT HIGH CO2	1	1		0.0003		0.0001	
	2	1		0.0026		0.0002	
	3	1		0.0054			0.0001
TEMP AT LOW CO2	1	1		0.0005			
	2	1					
	3	1					0.0231

Table 5.2. Results of ANOVA of gas exchange variables for Salix arctica in response to soil drying in controlled environments. *Because SLA was measured only after 19 d, there are no P values for within-subjects effects.

	DF	NA	Gs	WUE	WP	Ci/Ca	SLA
BETWEEN-SUBJECTS EFFECTS							
CO2	1	0.0001	0.1476	0.0813	0.1075	0.3554	0.1318
ERROR	14						
WITHIN-SUBJECTS EFFECTS							
TIME	7	0.0001	0.0001	0.3651	0.325	0.0001	
TIME X CO2	7	0.0001	0.0563	0.3632	0.7263	0.1628	
ERROR	98						

Figure 5.1. Gas exchange of Salix arctica under well-watered conditions in controlled environments. Bars represent means ± SE. N=24, 19, 21, and 16 for the HTHC, HTLC, LTHC, and LTLC treatments respectively.

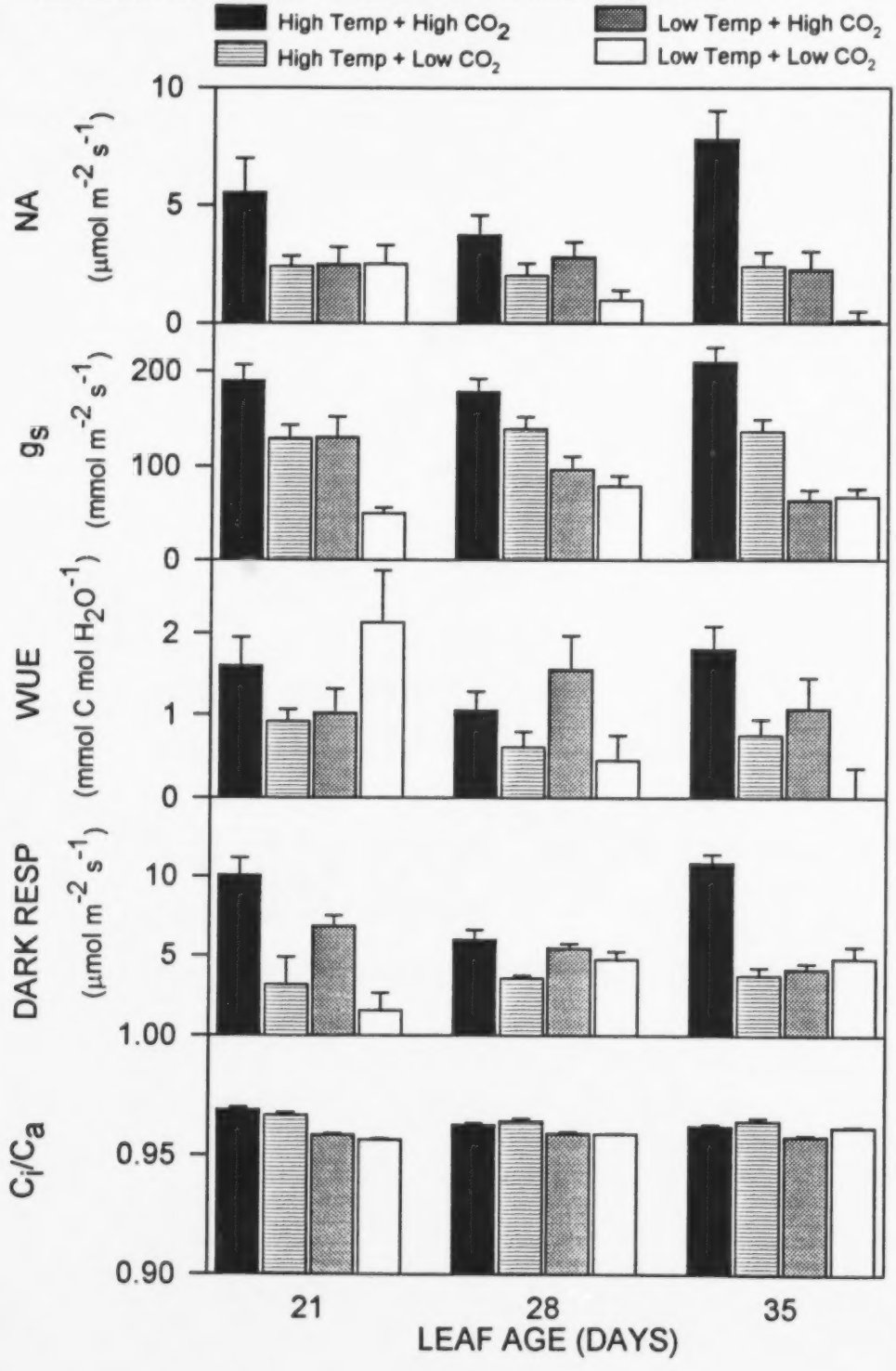


Figure 5.2. Specific leaf areas for Salix arctica under well-watered conditions and during the dry-down experiment in controlled environments. Bars represent means ± SE. N=9 and 7 for the HTHC and HTLC treatments respectively.

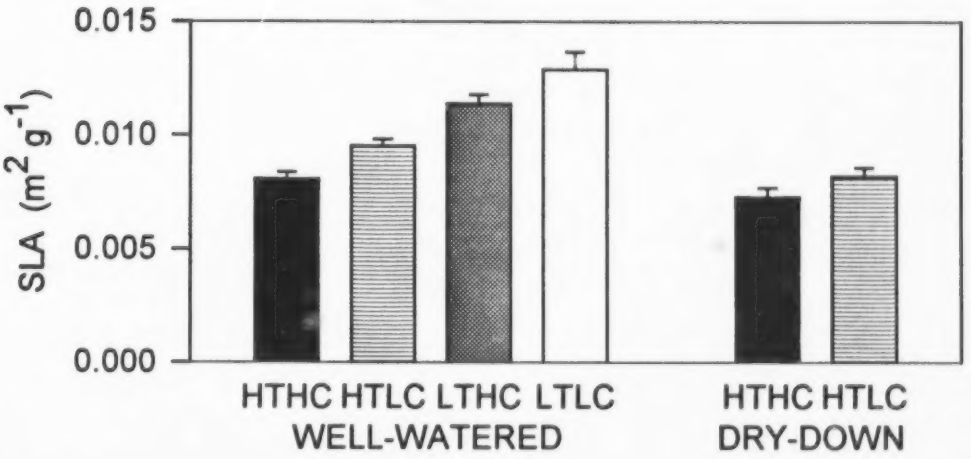
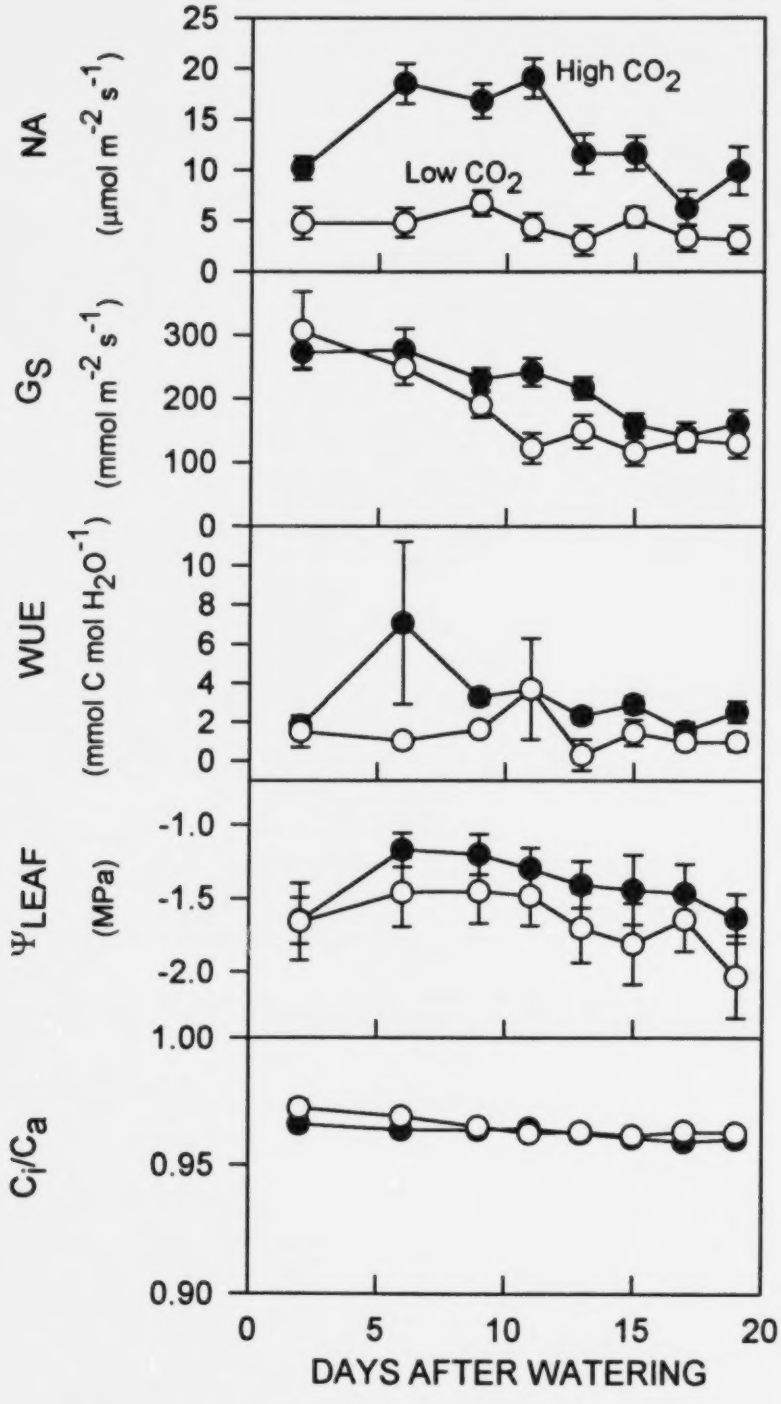


Figure 5.3. Gas exchange of Salix arctica in the dry-down experiment in controlled environments. Bars represent means ± SE. N=9 and 7 for the HTHC and HTLC treatments respectively.



References

Arp, W. J. 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO2. Plant, Cell and Environment **14**:869-875.

Billings, W. D., J. O. Luken, D. A. Mortensen, and K. M. Peterson. 1982. Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? Oecologia **53**:7-11.

---. 1983. Increasing atmospheric carbon dioxide: possible effects on arctic tundra. Oecologia **58**:286-289.

Bliss, L. C., and N. V. Matveyeva. 1992. Circumpolar arctic vegetation. Pages 59-90 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Bowes, G. 1991. Growth at elevated CO2: photosynthetic responses mediated through Rubisco. Plant, Cell and Environment **14**:795-806.

Chapin, D. M., and C. S. Bledsoe. 1992. Nitrogen fixation in arctic plant communities. Pages 301-320 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology **66**:564-576.

Chapin, F. S., III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver, and J. Svoboda, editors. 1992a. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, CA.

---. 1992b. Arctic plant physiological ecology in an ecosystem context. Pages 441-451 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Chaves, M. M. 1991. Effects of water deficits on carbon assimilation. Journal of Experimental Botany **42**:1-16.

Dawson, T. E., and L. C. Bliss. 1989. Intraspecific variation in the water relations of Salix arctica, an arctic-alpine dwarf willow. Oecologia **79**:322-331.

---. 1993. Plants as mosaics: leaf-, ramet-, and gender-level variation in the physiology of the dwarf willow, Salix arctica. Functional Ecology **7**:293-304.

Drake, B. G. 1992. The impact of rising CO_2 on ecosystem production. Water, Air, and Soil Pollution **64**:25-44.

Eamus, D., and P. G. Jarvis. 1989. The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. Pages 2-55 *in* M. Begon, A. H. Fitter, E. D. Ford and A. Macfadyen, editors. Advances in ecological research. Volume 19. Academic Press, London.

Farrar, J. F., and M. L. Williams. 1991. The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. Plant, Cell and Environment **14**:819-830.

Field, C. B. 1987. Leaf-age effects on stomatal conductance. Pages 367-384 *in* E. Zeiger, G. D. Farquhar and I. R. Cowan, editors. Stomatal Function. Stanford University Press, Stanford, CA.

Grulke, N. E., G. H. Riechers, W. C. Oechel, U. Hjelm, and C. Jaeger. 1990. Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. Oecologia **83**:485-494.

Guehl, J. M., C. Picon, G. Aussenac, and P. Gross. 1994. Interactive effects of elevated CO_2 and soil drought on growth and transpiration efficiency and its determinants in two European forest tree species. Tree Physiology **14**:707-724.

Henry, G. H. R., B. Freedman, and J. Svoboda. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. Canadian Journal of Botany **64**:2502-2507.

Henry, G. H., J. Svoboda, and B. Freedman. 1990. Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. Canadian Journal of Botany **68**:2660-2667.

Hilbert, D. W., T. I. Prudhomme, and W. C. Oechel. 1987. Response of tussock tundra to elevated carbon dioxide regimes: analysis of ecosystem CO_2 flux through nonlinear modeling. Oecologia **72**:466-472.

Idso, K. E., and S. B. Idso. 1994. Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the past 10 years' research. Agriculture and Forest Meteorology **69**:153-203.

Jones, H. G. 1985. Partitioning stomatal and non-stomatal limitations to photosynthesis. Plant, Cell and Environment **8**:95-104.

Jones, M. H., K. J. Greenway, S. M. Landhäusser, U. Silins, and B. Thomas. 1993. Creative solutions for little research problems. Bulletin of the Ecological Society of America **74**:251-253.

Kelly, D. W., P. R. Hicklenton, and E. G. Reekie. 1991. Photosynthetic response of geranium to elevated CO_2 as affected by leaf age and time of CO_2 exposure. Canadian Journal of Botany **69**:2482-2488.

Kielland, K., and F. S. Chapin III. 1992. Nutrient absorption and accumulation in arctic plants. Pages 321-336 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Kirschbaum, M. U. F. 1994. The sensitivity of C_3 photosynthesis to increasing CO_2 concentration: a theoretical analysis of its dependence on temperature and background CO_2 concentration. Plant, Cell and Environment **17**:747-754.

Limbach, W. E., W. C. Oechel, and W. Lowell. 1982. Photosynthetic and respiratory responses to temperature and light of three Alaskan tundra growth forms. Holarctic Ecology **5**:150-157.

Long, S. P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO2 concentrations: has its importance been underestimated? Plant, Cell and Environment **14**:729-739.

Maxwell, B. 1992. Arctic climate: potential for change under global warming. Pages 11-34 *in* F. S. I. I. I. Chapin, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, CA.

McGraw, J. B., and N. Fetcher. 1992. Response of tundra plant populations to climatic change. Pages 359-376 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

McNulty, A. K., and W. R. Cummins. 1987. The relationship between respiration and temperature in leaves of the arctic plant Saxifraga cernua. Plant, Cell and Environment **10**:319-325.

McNulty, A. K., W. R. Cummins, and A. Pellizzari. 1988. A field survey of respiration rates in leaves of arctic plants. Arctic **41**:1-5.

Meinzer, F. C. 1993. Stomatal control of transpiration. Trends in Ecology and Evolution **8**:289-294.

Morrison, J. I. L. 1987. Intercellular CO_2 concentration and stomatal response to CO_2. Pages 229-251 *in* E. Zeiger, G. D. Farquhar and I. R. Cowan, editors. Stomatal function. Stanford University Press, Stanford, CA.

Muc, M., J. Svoboda, and B. Freedman. 1994. Soils of an extensively vegetated polar desert oasis, Alexandra Fiord, Ellesmere Island. Pages 41-50 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis. Captus University Publications, Toronto.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and A. E. Linkins. 1992. Microbial processes and plant nutrient availability in arctic soils. *in* Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Norby, R. J., and E. G. O'Neill. 1991. Leaf area compensation and nutrient interactions in CO_2-enriched seedlings of yellow-poplar (Liriodendron tulipifera L.). New Phytologist **117**:515-528.

Oberbauer, S. F., and T. E. Dawson. 1992. Water relations of arctic vascular plants. *in* Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Oberbauer, S. F., N. Sionit, S. J. Hastings, and W. C. Oechel. 1986. Effects of CO2 enrichment and nutrition on growth, photosynthesis, and nutrient concentration of Alaskan tundra plant species. Canadian Journal of Botany **64**:2993-2998.

Oechel, W. C., and W. D. Billings. 1992. Effects of global change on the carbon balance of arctic plants and ecosystems. *in* Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Oechel, W. C., and B. R. Strain. 1985. Native species responses to increased atmospheric carbon dioxide concentration. Pages 117-154 *in* B. R. Strain and J. D. Cure, editors. Direct effects of increasing carbon dioxide on vegetation. U.S. Dept. of Energy, Washington, D.C.

Oechel, W. C., G. Riechers, W. T. Lawrence, T. I. Prudhomme, N. Grulke, and S. J. Hastings. 1992. 'CO_2LT' an automated, null-balance system for studying the effects of elevated CO_2 and global climate change on unmanaged ecosystems. Functional Ecology **6**:86-100.

Ögren, E., and G. Öquist. 1985. Effects of drought on photosynthesis, chlorophyll fluorescence and photoinhibition susceptibility in intact willow leaves. Planta **166**:380-388.

Porsild, A. E., and W. J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. National Museums of Canada, Ottawa.

Sage, R. F. 1994. Acclimation of photosynthesis to increasing atmospheric CO_2: the gas exchange perspective. Photosynthesis Research **39**:351-368.

Semikhatova, O. A., T. V. Gerasimenko, and T. I. Ivanova. 1992. Photosynthesis, respiration, and growth of plants in the Soviet arctic. Pages 169-192 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Shaver, G. R., and J. Kummerow. 1992. Phenology, resource allocation, and growth of arctic vascular plants. Pages 193-212 *in* F. S. Chapin III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego.

Silvola, J., and U. Ahlholm. 1992. Photosynthesis in willows (Salix x dasyclados) grown at different CO_2 concentrations and fertilization levels. Oecologia **91**:208-213.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W.H. Freeman, New York.

Stitt, M. 1991. Rising CO2 levels and their potential significance for carbon flow in photosynthetic cells. Plant, Cell and Environment **14**:741-762.

Strain, B. R., and R. B. Thomas. 1992. Field measurements of CO_2 enhancement and climate change in natural vegetation. Water, Air, and Soil Pollution **64**:45-60.

Svoboda, J., and B. Freedman, editors. 1994. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus University Publications, Toronto.

von Caemmerer, S., and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta **153**:376-387.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113-137 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York.

Woodley, E. J., and J. Svoboda. 1994. Effects of habitat on variations of phenology an nutrient concentration among four common plant species of the Alexandra Fiord Lowland. Pages 157-176 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, Ontario.

Woodward, F. I., G. B. Thompson, and I. F. McKee. 1991. The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. Annals of Botany **67**:23-38.

Wookey, P. A., A. N. Parsons, J. M. Welker, J. A. Potter, T. V. Callaghan, J. A. Lee, and M. C. Press. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. Oikos **67**:490-502.

CHAPTER 6

Summary

The studies reported here describe the initial, short-term responses of high arctic plants to experimental conditions simulating climate changes predicted to occur over the coming century. We examined the growth, phenology, and reproduction of arctic willow, Salix arctica, in response to experimental warming over the course of the first three years of a long-term field study. We measured the diurnal photosynthetic responses of this willow and two sedge species, Eriophorum angustifolium triste and Carex aquatilis stans, during the first two years of the field warming experiment. Finally, in controlled environments, we examined photosynthesis in S. arctica subjected to atmospheric CO_2 and temperature conditions which reflected current and predicted environmental changes. These studies were carried out at the functional level of the leaf and shoot, but explicitly examined variability introduced by sex, microsite, and habitat, as well as different temporal scales.

While the overriding goal of this work was to quantify the initial influence of temperature and atmospheric CO_2 on these species within a climate change context, a secondary goal was to provide a broader ecological interpretation that would help direct future studies of climate change in arctic ecosystems. Our research focused on the direct effects of enhanced temperature and atmospheric CO_2. Indirect effects of experimental warming in the field, such as changes in soil moisture regimes, deeper active layer, or increased nutrient mineralization, require detailed companion studies, and are currently under way or are planned for Alexandra Fiord. Nevertheless, our results are an important first contribution to the coordinated, long-term study of global climate change on tundra plant species. The data presented here will be included in the International Tundra Experiment database at the Danish Polar Center in Copenhagen, and will be used to help address additional questions of broader ecological importance or application.

The species examined in these studies do respond to relatively small increases in growing season temperature, as well as to elevated atmospheric CO_2, but the direction and magnitude of their responses clearly depend on sex, species, microsite, and habitat.

In Salix arctica, increases in catkin and leaf fascicle length, specific leaf area, and stem growth indicate that this willow responds favorably to ameliorated growing season temperatures, and that there is some cumulative effect of warming on growth over three years. However, these growth response variables were enhanced only in the dry habitat. Furthermore, the field photosynthesis measurements indicate that a positive influence of temperature was strongly dependent upon the sex of the plant and the habitat in which it grew. The colder soils and relatively later snowmelt in the wet meadow probably reduced the effect of warming in this habitat. The ability of willows in the meadow to increase their assimilation potential may be inherently lower than dry habitat plants, indicated by relative but admittedly weak differences within each experimental treatment in the common conditions of the controlled environments. More important, however, is the indication that elevated atmospheric CO_2 might not have an impact on net assimilation in S. arctica unless air and soil temperature is also sufficient.

Data from the sedge gas exchange study indicate that sedge species respond differently to warming, and indicate that the strength and direction of the response depend in part on small-scale environmental differences observable between hummock and hollow microsites. In this work, photosynthesis in Eriophorum angustifolium triste was depressed by warming, and the magnitude of the effect was greater for shoots growing on the warmer hummocks. In contrast, Carex aquatilis stans was not affected by warming, but plants growing on the warmer hummocks had significantly lower photosynthesis than those in the hollows. Further research is required to determine whether these responses represent ecotypic differentiation, which has the potential to play a critical role in how arctic ecosystems respond to climate change. It is apparent that current research, including ITEX, should

not ignore the potential of gender, microsite, and habitat to influence arctic ecosystems structure and function.

The impact of warming on willow reproductive potential is difficult to assess, since the OTCs themselves appeared to influence pollination and reproductive allocation. Further research is required to determine how warming will impact seed production and viability at Alexandra Fiord, particularly if we are to be able to make comparisons with other ITEX sites. Nevertheless, if nutrients and pollinators are not limiting, the catkin data relating length to staminate and pistillate flower numbers suggest that while potential seed production may remain unchanged, pollen production could be improved significantly. However, given the photosynthesis and growth data, only males in the dry habitat might benefit, and could gain a competitive advantage as pollen donors. Over the long term, differential reproduction, survival, or growth related to gender or habitat could have a substantial impact on community dynamics.

Other factors could offset any potential improvements in reproduction, particularly if female willows do not increase total seed production with warming. Increased activity of herbivores, particularly the Arctic woolly-bear caterpillar Gynaephora groenlandica at Alexandra Fiord, and muskox at other locations, could substantially reduce any potential increase in viable seed production by consuming catkin (and leaf) buds early in the season. Whether seeds would have the opportunity to germinate and become established would of course depend on the availability of suitable safe sites. The field germination tests clearly indicate that germination is favored on the moist substrate in the meadow. However, disturbances which could open the dense vegetation that currently exists in the meadow, are unlikely at Alexandra Fiord. Solifluction and anthropogenic surface disturbances are more common elsewhere in the arctic.

Taken together, the results of this research are equivocal in the picture they construct of how Salix arctica, in particular, is likely to respond to future climate change. The strengths of the short-term, direct responses to warming

and atmospheric CO_2 are not large, but do appear to be cumulative for some response variables. Whether they would translate, over the long term, into additional growth, reproduction, or survival in the field, or would confer some competitive advantage, is entirely unclear. Community-level changes in species composition of arctic tundra may be more likely than large changes in growth or reproduction, particularly if some species, such as Eriophorum angustifolium, and female willows in the meadow, are negatively influenced by a changed climate. We agree with other researchers who conclude that indirect effects of warming would probably have a stronger impact on tundra vegetation than direct effects (Chapin et al. 1992). For example, even if Salix arctica does respond positively to enhanced CO_2 and ameliorated growing season temperature, decreases in soil moisture or nutrients would probably limit the magnitude of its response. The natural climatic variability at Alexandra Fiord (Labine 1994) likely influenced the seasonal growth and reproductive responses of S. arctica during the three years of this study.

If we were to predict some generalized population and community changes in the habitats we studied at Alexandra Fiord, we might make the following predictions. In the dry habitat, we would expect to see little substantial change in willow growth, or in the importance of willows in community composition unless precipitation regimes change markedly or other species respond very strongly to environmental changes. Significant increases in snowfall could decrease growing season length, in which case growth would be slowed and sexual reproduction curtailed, in part due to climatic effects on pollinators. Small increases (or decreases) in snowfall would only have an impact on this community if wind patterns change and fail to blow most of the snow away during the winter as under current conditions.

Because the lowland at Alexandra Fiord is one of the warmest locations in which Salix arctica grows in the Canadian High Arctic, we have no natural analogue for examining the effect of an even longer growing season on the growth of this species. However, growth differences between the dry and wet habitats, although confounded by other environmental differences including

soil temperature and moisture, suggests that a lengthened growing season could have a positive impact on willow growth and reproduction. If the growing season is extended only by warmer temperatures in the autumn, or plants respond to elevated atmospheric CO_2 by delaying senescence, the benefits for growth and reproduction would be minimal, and damage from early frosts more likely. Relatively low soil moisture, localized in this habitat by virtue of topography, could be exacerbated if changes in precipitation patterns do not mitigate drying, but Salix arctica presently tolerates conditions of low soil moisture at Alexandra Fiord and other locations. If increased precipitation has a positive effect on soil moisture, willow growth would probably improve. Either way, relative differences in survival between sexes would probably not become pronounced in this habitat. Increased secondary metabolites might mitigate any increases in herbivory, particularly if soil nutrients remain limiting. However, other changes in species composition in this community would probably occur if soil moisture regimes were appreciably altered; for example, Oxyria digyna, which appears more sensitive to limitations in early-season soil moisture availability than Salix arctica, might not persist in this particular habitat.

There is greater uncertainty regarding the wet meadow, primarily because of the uncertainty regarding the potential for substantial changes in soil moisture in this habitat. Increases in temperature and precipitation could maintain soils in a hydric state, since current soil moisture is influenced strongly by effects of insolation on runoff from higher elevations. In the first year of these studies, the summer was relatively cloudy and cool and the meadow was more mesic than wet. In subsequent years, better weather caused surface water flow to cover a much greater area of the meadow. If generally saturated soil conditions remain unchanged, but are accompanied by elevated air temperature, then the impact on willows and Eriophorum could be substantially negative over the long term. On the other hand, if soil moisture was reduced, by a combination of factors involving reduced surface flow and increased active layer depth, then the negative effect on willows might be

eliminated, while the effect on Eriophorum might be become more pronounced. Sedge tiller production is enhanced by temperature and CO_2 (Henry et al. 1986, Tissue and Oechel 1985), which could increase competition for nutrients, depending upon how much mineralization and N-fixation occurs with soil warming and drying.

Can these predictions be extrapolated to other high arctic communities? Alexandra Fiord lies near Greenland's semi-permanent high-pressure system, and in the orographic shadow of Ellesmere Island's central mountains (Labine 1994). Moreover, soil moisture is generally higher throughout the lowland than in most other high arctic locations, in part due to higher organic matter content (Muc et al. 1994). Consequently, conditions at Alexandra Fiord are different than elsewhere on Ellesmere Island, and it is difficult to extend our observations to other, non-oasis locations.

Like Alexandra Fiord, the Fosheim Peninsula is also a polar oasis, but on a much larger scale and with substantially different topography. Although this region has slightly fewer growing degree-days and less net radiation than Alexandra Fiord (Labine 1994), vegetation here might respond similarly to that at Alexandra Fiord. In polar desert or semi-desert environments, such as that found in the middle of Sverdrup Pass, Ellesmere Island, limited soil moisture and strong winds would continue to have a large impact on Salix arctica, and would be likely to influence overall community composition by reducing the number of species present. In other non-oasis locations, willow density and cover is often dependent upon substrate type (Bliss et al. 1994), and substrate quality may be more important than temperature for increasing soil nutrient mineralization with climate change (Nadelhoffer et al. 1991). Climatic changes would probably have different effects in grazed ecosystems. Heavy grazing by muskox results in substantially less willow cover and biomass, and also prevents formation of the hummock-hollow complex found in ungrazed systems like Alexandra Fiord. Organic matter, nutrient concentrations, and species composition are substantially different in grazed versus ungrazed sedge meadows (Henry and Svoboda 1994). In raised beach ridge communities

typical at Truelove Lowland on Devon Island, reductions in soil moisture could reduce willow productivity. In the wet and mesic meadows below these ridges, additional snow accumulation could substantially shorten the growing season. Shifts in habitat partitioning based on sexual differences in the willows could also be possible (Dawson and Bliss 1989).

This work identified or confirmed the need for further research in two key areas. First, it is clear that indirect effects of climatic change in the High Arctic could substantially modify the responses of the plant species we observed in these studies. If we are to succeed in modeling ecosystem response to climate change at Alexandra Fiord, and particularly if we are to understand the feedback mechanisms between plants and ecosystem function, we need a firmer understanding of four critical components: how soil moisture regimes will change in different habitats, how this will influence soil nutrient availability, whether growing season will change appreciably, and how much of an impact herbivory might have on certain key species. Second, the effects of sex, microsite, and habitat must also be addressed in more detail. We need to confirm whether the variability in response we observed at these different scales in fact represent ecotypic differentiation or other heritable traits, and whether patterns exist among latitudinal or elevational gradients, or among life-forms. Although we observed significant short-term effects of these factors on photosynthesis and growth of our study species, and recognize the potential for substantial long-term effects, the question remains whether population or community differences would grow in magnitude or would somehow be mitigated with time.

References

Bliss, L. C., G. H. R. Henry, J. Svoboda, and D. I. Bliss. 1994. Patterns of plant distribution within two polar desert landscapes. Arctic and Alpine Research **26**:46-55.

Chapin, F. S., III, R. L. Jeffries, J. F. Reynolds, G. R. Shaver, and J. Svoboda, editors. 1992. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, CA.

Dawson, T. E., and L. C. Bliss. 1989. Patterns of water use and the tissue water relations in the dioecious shrub, Salix arctica: the physiological basis for habitat partitioning between the sexes. Oecologia **79**:332-343.

Henry, G. H. R., and J. Svoboda. 1994. Comparisons of grazed and non-grazed high-arctic sedge meadows. Pages 193-194 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, ONT.

Henry, G. H. R., B. Freedman, and J. Svoboda. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. Canadian Journal of Botany **64**:2502-2507.

Labine, C. 1994. Meteorology and climatology of the Alexandra Fiord lowland. Pages 23-40 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, ONT.

Muc, M., J. Svoboda, and B. Freedman. 1994. Soils of an extensively vegetated polar desert oasis, Alexandra Fiord, Ellesmere Island. Pages 41-50 *in* J. Svoboda and B. Freedman, editors. Ecology of a polar oasis. Captus University Publications, Toronto.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and J. A. Laundre. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology **72**:242-253.

Tissue, D. T., and W. C. Oechel. 1987. Response of Eriophorum vaginatum to elevated CO_2 and temperature in the Alaskan tussock tundra. Ecology **68**:401-410.

Appendix A

Monthly mean climate variables from a meteorological station in the wet meadow at Alexandra Fiord, for the years 1992-1994.

		AIR TEMPERATURE			SOLAR RADIATION	WIND SPEED
YEAR	DATES	MEAN	MAX	MIN	W/M^2	M/S
1992	JUNE	2.1	4.8	-0.7	289.1	2.1
	JUNE 15-30	4.4	7.3	1.4	296.1	2.1
1993	JUNE 15-30	5.2	8.3	2.0	263.8	2.1
	JULY	7.2	10.3	4.0	231.3	1.3
	AUGUST	2.8	5.7	-0.3	117.8	2.0
	AUGUST 1-13	3.6	6.5	1.1	130.8	2.8
1994	JUNE 15-30	4.3	7.0	1.3	251.5	2.4
	JULY	5.2	8.1	2.1	238.6	2.4
	AUGUST	6.0	9.6	2.5	203.8	1.9
	AUGUST 1-13	5.8	10.0	2.3	144.4	2.0

NOTES:

1. July 1992 to June 1993 data missing due to datalogger failure.
2. Datalogger reinstated on 14 June 1993, hence data only for 15-30 June.
3. Most recent data recovered on 14 August 1994.
4. Air temperature from shielded thermistor at 2 m.
5. Solar radiation measured with silicon pyranometer (LiCor 2000) at 3 m.
6. Windspeed measured with anemometer at 3 m.